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THE FLIGHT ACTIVITIES OF THE HONEYBEE[1]

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INTRODUCTION

Although the flight of honeybees to and from the hive has attracted the attention of students of beekeeping from the earliest times, no detailed study has been made, so far as can be determined from the beekeeping literature, of the actual number of flights from a colony of bees or of the variations which occur in these flights with changes in external environmental factors. Obviously it is extremely difficult to obtain even a small number of accurate records by counts made at the entrance of the hive. Therefore, to obtain adequate scientific data for a thorough study of the problems pertaining to the flight of bees it is essential to have some mechanical means which will automatically register the exits and returns of the bees over long periods of time.

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[1] This paper was prepared in part fulfillment of the requirements for the degree of doctor of philosophy at Cornell University. While engaged in this work the author held a Government overseas scholarship from the Department of Agriculture of the Union of South Africa. The work was done in cooperation with the Bee Culture Laboratory of the Bureau of Entomology, at Somerset, Md. The writer is indebted to the Carnegie Fund of the Imperial Bureau of Entomology, London, and to the Department of Agriculture, Union of South Africa, for financial assistance. He was regularly assisted in the taking of data by Miss Effie Ross and from time to time by other members of the Bee Culture staff. He also gladly acknowledges his indebtedness to Prof. F. Y. Edgeworth, All Souls College, Oxford, several of whose published articles have been found of value, and to Prof. H. H. Love, Cornell University, and Dr. G. W. Vinal, Bureau of Standards, for helpful suggestions.

While reading an interesting paper by Léon Dufour,[2] in which are shown the great variations which the weight of a hive undergoes in the course of a single day, the writer, seeing how the incoming nectar and pollen modified the interpretations of the flights which occurred, realized more fully the scientific value of an automatic apparatus which would register the exits and returns of the individual bees, and was led to spend the greater part of the winter of 1921–22 in devising an apparatus for this purpose.

Actual recording of individual flights was begun on April 8, 1922, with 14 units of the apparatus in place. On May 10 the full quota of 30 instruments was installed and readings were continued regularly, including Sundays and holidays, from daylight to dark, until July 29, except for six days, when the work was interrupted by certain necessary modifications or adjustments of the apparatus. During this period some five million flights to and from the hive were recorded, the gross weight of the bees representing half a ton.

Since the first object of this experiment was to determine the practicability of obtaining data on problems pertaining to the flight of bees by means of an automatic recording mechanism, rather than to make a study of any one of these problems, and since there appears to be no immediate opportunity for the writer to continue this interesting line of investigation, it seems best to record the data so far obtained, that they may serve as at least an introduction to a further study of this phase of bee behavior.

THE APPARATUS

At the outset it was clear that, on account of the limited space at the hive entrance, the most practical apparatus for counting the flights of bees would be one in which each bee would establish electrical contact as it left or as it entered the hive. Any such apparatus must consist of as many units as will accommodate the full flight of the colony under experimentation, each unit consisting of one contact device and one recording mechanism.

THE CONTACT DEVICE

A device for establishing electrical contacts that will give the desired data is one which requires for its operation little or no exertion on the part of the bee and which will delay the bee very little or not at all in its departure or return. To meet these requirements there are at least three possible methods of approach, arranged here in the ascending order of their complexity and expense.

(1) To allow the bee to push against some mechanism.

(2) To allow the weight of the bee to operate some mechanism.

(3) To use a minute electric current, the circuit of which is closed by the body of the bee itself as it passes the terminals, but not strong enough to cause any modification of behavior, and then to amplify this current so as to operate the recording mechanism.

Working on the plan of allowing the bee to push against some mechanism, a modification of the ordinary bee-escape which allows bees to pass but one way was tried. A small wire was soldered at right angles to one of the springs, so that as the bee passed between the springs this wire was pushed into a small cup of mercury, thus closing the electric circuit. It is a simple enough matter to get a bee to form such a contact, but to get each contact to represent the passage of but one bee proved to be exceedingly difficult and is perhaps impossible. Seven different devices of this sort were constructed and tested, each intended to overcome some defect inherent in those preceding. Regarding these devices, it suffices to say that none of them proved practical. One of the chief difficulties was the fact that the springs may be so delicately adjusted that on the passage of a bee a contact may be formed by the head and thorax and then another contact formed by the abdomen. Yet another bee passing these same springs in a slightly different manner may get through without forming any electrical contact whatever. An attempt was made to overcome this difficulty by taking advantage of the smaller constriction which exists between the dorsal surface of the propodeum and the abdomen; that is to say, the bee was forced to walk in an upright posture, through a tube of special cross section, so that the spring passed over this dorsal region. The bees, however, showed great reluctance to go through such a tube.

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[2] Dufour, Léon. Travail des butineuses et récolte du miel. *In* L'Apiculteur, vol. 41, no. 8, pp. 300–312. 1897.

George S. Demuth and N. E. McIndoo, both formerly connected with the Bee Culture Laboratory, have informed the writer that they, too, have given some thought to this problem. Mr. Demuth attempted to get the bees to push against prongs placed equidistant around a revolving wheel, much on the principle of the undershot water wheel. Doctor McIndoo tried to get the bees to push against small hinged gates. Neither attempt was carried to completion.

Owing to the fact that the stimulations of bees to flight, such as light intensity, nectar flows, and other environmental factors, vary greatly in degree, and also that individual bees apparently differ somewhat in their reactions to even slight obstacles placed in their way, it is questionable whether any apparatus working on the principle of having the bees push against a mechanism will ever be found practical.

Attention was then turned to the possibility of utilizing the weight of the bee to form an electrical contact. Three models were constructed on this plan, each proving to be a step in advance. The third model, after several long tests, appeared to be the instrument required. After a few minor improvements in the design, 30 such instruments were built, 15 to accommodate outgoing bees and 15 for incoming. These instruments are referred to in this paper as "gates."

This device (fig. 1) may be described as a miniature balance on jeweled pivots. As the bee enters the tunnel fixed to one end of the lever, its weight, having a greater moment than the counterbalance, causes the tunnel to drop and this movement produces three consecutive results: (1) It closes the door to prevent a second bee from gaining entrance to the case while the tunnel is on its downward stroke; (2) it establishes an electric contact by thrusting two platinum prongs attached to but insulated from the lever, into two mercury cups; and (3) it opens a second door on a lower level, permitting the bee to fly to the field or to enter the hive, as the case may be. The bee having left the tunnel, the counterbalance now has a greater moment than the empty tunnel, the second door is closed, contact is broken, and the first door is opened, so that the mechanism is now ready to count the next bee. This seesaw motion continues as long as bees are passing through the tunnel. The illustration (fig. 1) shows an incoming gate. The only difference between this and an outgoing gate is the presence of glass immediately in front of the tunnel on the outgoing gate, and a different position of the binding posts. The tunnels adopted after some experimentation were 15 millimeters long, from 6.5 to 7 millimeters wide, with a curved upper portion from 4.5 to 5 millimeters at the highest point. These were so adjusted that a 67-milligram weight placed at the base of the rear door brought the tunnel down to the lower stop. At other times 75-milligram and 47-milligram weights were used, but most of the data were obtained with the first-mentioned adjustment.

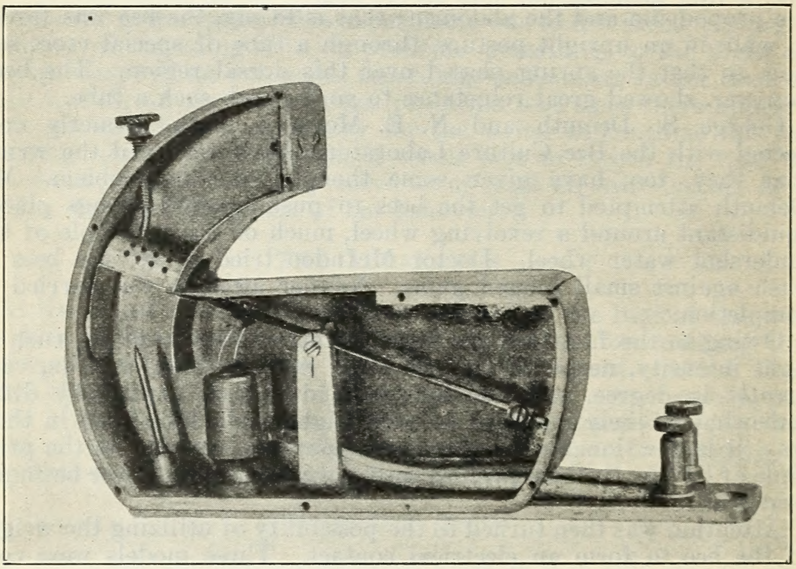

FIG. 1.—Apparatus for recording by electrical contact the ingress of bees into the hive

Since this device, in the course of this investigation, has shown certain undesirable features, it remains, in a search for the ideal counting device, to consider briefly the possibility of counting bees by means of the amplification of a current whose circuit is closed by the body of the bee itself.

In discussing the possibility of this method with the writer, radio experts have suggested that it might be better to get the bee to pass between the plates of a small condenser and thus to vary its dielectric constant, and then to use this variation to record the passage of the bee. Assuming that expense is of no consideration, it is still questionable whether this method would have any advantage over the one used in this investigation. Some device would be needed before and after the condenser to regulate the passage of the bees, and these obstructions might be as great as or greater than that offered by the present device, so that the only advantages to be gained, provided the principle could be developed to do away with occasional multiple recording by the same bee, would be a less frequent necessity for cleaning the gates, and perhaps a relatively larger capacity for each gate.

THE COUNTING DEVICE

If the bee-escape method of counting had proved successful, it would have been necessary to use a weak current for making the records. The first type of counter tried consisted of an ordinary alarm clock with the balance wheel removed. A piece of soft iron was then attached to the escape lever and an electromagnet was placed on the framework. When this magnet was excited by the closing of the circuit by the bee, it attracted the soft iron on the escape lever and allowed one tooth of the escape wheel to pass. When contact was broken, a light spring brought the lever back to its first position. Thus one contact corresponded to one vibration of the original balance wheel, and by knowing the beat of the clock it was possible to count the exits or entrances from any particular gate merely by reading the " time " on the dial.

This instrument, though crude, proved promising, but was not adopted for the present investigation. With the balance device adopted, a much stronger current can be used. It was therefore possible to use a telephone-message register, already manufactured and available, which consists of a simple cyclometer actuated by an electromagnet, operating on a higher voltage (about 16 or 18 volts) than would be required for the counter made from the clock.

ARRANGEMENT OF THE APPARATUS

For convenience in handling, each set of gates was attached to a board hinged to the end of a 10-frame Langstroth hive body, so that the instruments could be swung away from the hive and yet not be detached entirely. When these boards were clamped to the hive, so as to close the entrance, the outgoing gates were above and somewhat in front of the incoming ones, the actual exit apertures being about 2 inches above the row of entrance apertures. This arrangement proved very satisfactory, because it minimized the possibility of the bees holding down the tunnels of outgoing gates by attempting to enter the hive through them.

A false bottom-board within the hive conducted the bees to the outgoing instruments, and an outside alighting-board led the returning bees to the ingoing tunnels. The incoming bees, on passing through the contact mechanism, entered a small chamber below the inside false bottom-board, and to enter the brood chamber proper they passed through slots in this false bottom-board. A strip of queen-excluding zinc was placed behind the outgoing gates and above the slots at an angle of about 45°, sloping upward and backward. This forced the bees in carrying their dead to drop them, so that the dead bees fell through the slots in the false bottom-board to a position behind the incoming gates, where they could conveniently be removed and counted.

Ventilation was at first provided by means of a maze which admitted air but no light through a slot in the bottom-board. This arrangement proved satisfactory until some time in June, when a change was necessitated by the peculiar behavior of the bees during hot weather. Several changes were tried, but the plan that appeared to give the greatest satisfaction was to close this lower ventilator and to remove one of the ingoing gates, the remaining 14 gates being spaced more widely, thus allowing more of the hive odor to escape between the gates. Ventilation at the top of the hive was also provided during the hottest weather.

A weatherproof telephone cable led the wires from the contact devices to the recording counters attached to a table in the laboratory, about 50 feet from the hive. Two storage batteries furnished the current, these being recharged periodically by means of a rectifier.

During the portion of each day when the bees were flying, the following observations were recorded without interruption at exactly 15-minute intervals: Records of outgoing and incoming bees; weight of the entire hive with attached apparatus; temperature in the shade adjacent to the hive; anemometer record of the wind which had passed since last reading; and notes on the weather conditions, including the degree of cloudiness. These readings usually began at about 5.30 a. m. and continued until about 8 p. m., depending somewhat on the season.

PROBLEMS ON WHICH INFORMATION MAY BE OBTAINED BY A DEVICE FOR COUNTING FLIGHTS

If an accurate count could be obtained of the exits from and entrances to a hive without interfering unduly with the normal flight activities of the bees, the data obtained would throw some light on the following problems:

1. Perhaps the most important would be the responses of bees to various honey flows, especially to those that are not heavy enough to be reflected very markedly in the weight of the hive. Information regarding this problem would undoubtedly assist in a study of nectar secretion, especially with reference to the time of day and the relative amount of secretion.
2. The responses of bees to various meteorological conditions, such as intensity of light, temperature, wind, rain, and electrical disturbances.
3. Average duration of the flight, its variation with the honey flows and the general atmospheric conditions.
4. The daily average number of trips per bee to the field, ascertained by manipulating the hive so as to get a census of the field bees on any particular day.
5. The possible responses of bees to sounds, odors, and other stimuli.
6. The death rate of the colony, the comparative numbers which die in the field and in the hive, and the factors which contribute to an increased death rate.
7. The effect on bees of the time of application of certain poisonous insecticides in horticultural practice.
8. The relative economic importance of predatory wasps, other enemies, and adult bee diseases, information regarding which might be obtained by correlating flight data with the normal death rate.

THE CONDITIONS OF THE EXPERIMENT

In order to care for the great rush of bees on the approach of storms or to allow for possible clogging of some of the gates, it was necessary to provide such conditions that the gates would be worked normally much below their full capacity. This was done by employing a colony of bees of comparatively small size. When the taking of the records was begun in April, this colony, headed by a 1-year-old Italian queen, was in a hive composed of two bodies. The colony had about 5 pounds of bees, brood to fill four frames completely (Langstroth size), and seven frames containing honey. The remaining frames were nearly empty. When the colony was examined in detail on May 25, seven frames of brood and two frames containing eggs were present. A considerable number of larvæ then showed symptoms of sacbrood. On the termination of the experiment at the end of July there were about 3 pounds of adult bees, three frames of brood, and a serious shortage of honey. Some of the larvæ dead of sacbrood were not yet cleaned out.

To prevent so far as possible the drifting of other bees to this colony, the hive was set up in an isolated position about 36 feet from another colony and about 100 feet from the main yard on the west side of the bee culture laboratory, Somerset, Md. It was shaded by the building until 9 to 10 a. m. and by a tall tree in the afternoon.

During April, 1922, the hive did not show any days of gain in weight due to incoming nectar. In this region the main honey flow comes rather early, the two main nectar sources being black locust (*Robinia pseudacacia*) and tuliptree (*Liriodendron tulipifera*). These species yield nectar in May, usually early in the month, followed by a small amount of nectar from white clover (*Trifolium repens*) and from other plants of minor value for nectar. Usually by the end of June in this region a dearth of nectar occurs and lasts until fall, so that there is nothing for the bees to gather during midsummer, unless, as sometimes happens, there is a production of honeydew.

In the season of 1922 the first gain in weight from black locust occurred on May 3, but a heavy rain on the night of May 14 brought this honey flow to a sudden close. The tuliptree began to bloom on May 7, and the last gain from this source occurred on May 28. During this period of substantial honey flow there was no gain on five days because of rain. Small gains in weight from incoming pollen, with some nectar, took place in this colony on June 8, 10, and 17. All the other days throughout June and July showed a daily loss in weight, with the exception of July 16, when in the evening the hive had exactly regained its morning weight. The highest daily gain recorded for this colony was 1.440 kilograms, and on two other days the gain exceeded a kilogram. If a colony of full strength could have been employed the gains in weight would have been larger.

Of the 50 days on which this colony showed a loss in weight and on which rains did not invalidate the scale readings by the accumulation of moisture on the hive, 9 days showed a loss of 10 to 90 grams, 15 a loss between 100 and 190 grams, 8 between 200 and 290 grams, 13 between 300 and 390 grams, and 4 between 400 and 490 grams, with 1 day showing a loss of 610 grams. The experiment was discontinued before the beginning of the autumn honey flow.

For convenience in compiling the data, the quarter-hourly readings were recorded by means of a typewriter on cards of three different colors, blue being used for the outgoing data, yellow for the incoming data, and white for all other records and general notes. The differences between the successive readings and other data were obtained at a later date by the use of an adding machine. The long days, with frequent observations and the dismantling and cleaning of some of the gates in the evenings to get the apparatus ready for the following day, not only necessitated two observers but also rendered it impossible to make compilations during the active season of work.

FACTORS INTRODUCING ERRORS IN THE COUNT

With any untried experimental mechanism consisting, as this did, of many units, each unit in turn possessing parts having defects either of construction or of design, it is too much to expect perfect accuracy during the first season. Before discussing the magnitude of the experimental error produced by these deficiencies, it is desirable so far as possible to know the manner in which this error arises.

1. After observing the passage of about 2,000 bees through the early experimental model, it was thought that a tunnel had been devised which although allowing only one bee to pass at a time, would cause little inconvenience to the insect and would avoid as much as possible the scraping off of the load of pollen as the bee passes through the device. However, further experience with the full set of gates on the hive showed that some of the tunnels would occasionally allow two bees to pass at one time. Sometimes the two bees would get through and establish only one electrical contact, but they might cause two or even more contacts because of the irregular manner in which the tunnel fell under their weight, the movement being impeded by the pressure of their bodies against the stationary surfaces of the apparatus. Under normal weather conditions this difficulty was confined almost entirely to the outgoing gates, as the stimulus urging the bees into the outgoing channels was apparently much stronger than that attracting them into the ingoing tunnels. By darkening the glass windows and reducing the dimensions of the tunnels, this error was reduced to a minimum. Rebuilding all these tunnels was a tedious operation, consumed a great deal of time, and could be done only gradually, so that the early records show a greater error from this cause than the later ones.

2. Rebounding of the empty tunnel so as to form a second contact occurred occasionally if the adjustment of the counterweight was too delicate or if it had been rendered so by débris or pollen collecting in the tunnel.

3. Débris dropped or propolis placed by the bees in the clearance between the movable and stationary parts may cause double contacts by slowing down the speed of the tunnel in its fall; but when the quantity of débris became so large that the tunnel ceased to function, no error was introduced.

4. The voltage made necessary by the adoption of the telephone-message register unfortunately caused a considerable amount of oxidation on the surface of the mercury through arcing. In spite of frequent cleaning of the surfaces of mercury, this occasionally gave

some trouble in case the mercuric oxide collected as a flocculent mass on the platinum points. Under such circumstances the weight of the bee is no longer sufficient to overcome the greater displacement of mercury now necessary, and multiple contacts may result. This error was apparently eliminated by adjusting the apparatus so as to bring the mercury cups closer to the fulcrum, giving the bee a greater moment than this opposing force.

5. The bees about to enter the tunnel may push against the closed inner door (especially if its clearance is large) and may occasionally produce multiple contacts when the tunnel is either on its downward or on its upward stroke.

6. A bee pushing hard against the glass of an outgoing gate may produce multiple contacts by preventing a tunnel from falling rapidly past its critical point. Errors from this cause and from pushing against the closed inner door were very much reduced by darkening the glass on the gates (p. 8).

7. Bees clawing at the closed outer door of the device may bring the tunnel down far enough to form an electrical contact, especially if the doors are roughened by dirt or propolis or by a corrosion of the surface of the metal. Error from this source was peculiar to the ingoing gates, for on only two occasions was it observed on an outgoing gate. An attempt was made to eliminate this source of error by placing small metal cups over the exit hole so that clawing could take place only in an upward direction.

8. The segments of some of the recording cyclometers would sometimes bind against each other, thus failing to record the contacts when the magnet was excited by the passage of a bee. This necessitated some readjustments of the cyclometers.

9. The cleaning of the gates in the evening, after the day's records had been taken, necessitated the use of an artificial light, which on warm nights attracted some bees from inside the hive. These might remain outside all night, thus introducing an error on the following day.

10. The clustering out of the bees in the warm weather following the main honey flow was one of the most disturbing features of this investigation. On many days, records which were normal during the early part of the day were rendered valueless later on through the clustering out of the bees in the afternoon. At the same time this clustering out occurred throughout the apiary.

11. In the construction of the outgoing gates a small strip of metal was left between the outer aperture and the lower edge of the glass window, which was sometimes grasped by the bee in its fall, giving rise to multiple contacts.

12. A small error was caused by the actual drifting of the bees. This was apparent on colder mornings when the other hives in the apiary were active and the experimental one had not yet commenced its activity.

It is clear from the preceding list of causes of errors that with the exception of No. 8, and sometimes of No. 1, all these factors have a tendency to increase rather than decrease the recorded exits and entrances of the bees. With the experience gained in the 1922 season in the design and handling of this apparatus, the writer is convinced that, with the exception of Nos. 2 and 3, where débris is the cause of error, all these factors may eventually be eliminated.

On any particular day the magnitude of the experimental error depends upon the combination of factors operating on that day. On 89 of the 105 days on which records were taken, omitting records accidentally falsified by various causes, it appears that out of every 100 of the 2,434,666 contacts formed by outgoing bees, 96.84 returns were registered. On 37 of these days the records show more bees coming back than were recorded as going out, and these so-called gains in the returns give an obvious error of at least 1.86 per cent for the days recorded in Table 1. These 37 days were distributed as follows, and showed for every 100 exits daily the following average returns for each group: April, 4 days, 111.99; May, 10 days, 104.50; June, 7 days, 104.87; July, 16 days, 104.29. These data give some idea of the magnitude of the daily experimental error which may take place. The percentage returns on these days varied from 100.08 to the maximum, one day in April, when they were as high as 127.81.

If the days are selected on which the apparatus worked well, and the daily percentage of error which occurred, so far as it could be determined, is kept in mind, the general utility of the curves obtained from these data for such purposes as a study of the effect of external environmental factors is little affected by this error. For a study of the average duration of each flight, where a greater degree of accuracy is essential, a closer selection of data is necessary. Referring, therefore, to the outline of the problems on which it is hoped that such an apparatus may give some information, it is found that this apparatus is performing its function as regards four of them, one of which has been rated as the most important in this investigation.

FACTORS INFLUENCING THE FLIGHT

The various activities of the colony population are so interrelated that in a study of any one factor, influencing any particular activity such as flight, it sometimes becomes exceedingly difficult to gauge its exact influence, or even to give the right factor the credit for the behavior observed. Since it is possible not only to observe the variations in flight produced by changes in the intensity of any single factor throughout the course of a day, but also to gauge to a certain extent the gross influence of this factor on the day's flight as a whole, it is necessary in a study of any factor to make use of both of these sources of information. To ascertain the gross influence of any factor, a general survey of the whole period in which records were made is necessary.

THE SEASONAL SURVEY

In order to obtain a comprehensive picture of the daily flight activities throughout the season, it is necessary to plot a curve (fig. 2) of the total daily exits from the hive (Table 1). As might be expected, this curve has several high points, representing the data for those days when the conditions for flight were at an optimum for the period of the season in which they occur. A day that is considered an optimum for April would very naturally be a bad flight day for June or July; therefore in a study of any particular day a comparison must be made between this day and another in close proximity to it, when presumably, or as far as can be ascertained, the field conditions, internal conditions of the colony, and the number of field bees are but little different. By conecting these high points in the flight curve, there is obtained a second curve (fig. 2) indicating the optimum seasonal flight possible. This optimum curve, from the end of April to the first week of the honey flow in May, shows a fairly steep ascent (rising from 10,000 or 20,000 exits to 60,000 or 70,000 exits daily), indicative of the increasing number of field bees and their increased number of trips on the advent of the honey flow.

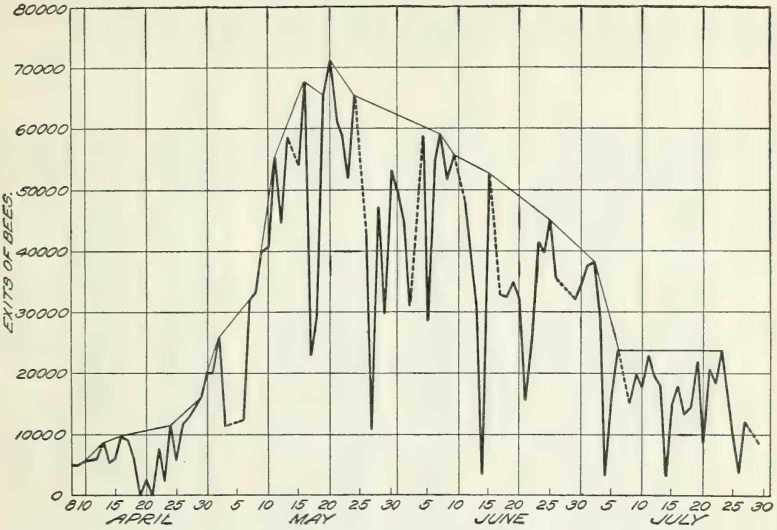

FIG. 2.—Total number of exits of bees from hive on each day during the period of investigation. Dotted lines indicate days on which no records were taken

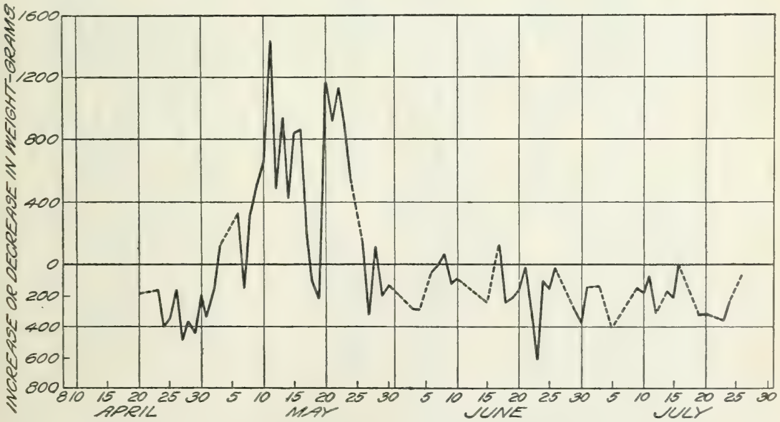

FIG. 3.—Graphical record of daily gains and losses in weight of the hive. The dotted portions of the curve indicate days on which weighings were not made, or were vitiated by moisture on the hive

Figure 3 illustrates another phase of the seasonal survey by presenting the increase or decrease in weight of the hive during the greater part of the period of investigation.

TABLE 1.—*A seasonal survey of some observations for entire days*

Date	Total exits	Total returns	Loss	Gain	Per cent returns are of exits	Loss or gain in weight of hive [1]	Average load per returning bee [2]	Per cent of possible sunshine	Temperature in shade during period of observations			
									Minimum		Maximum	
						Grams	Milligrams		°C.	°F.	°C.	°F.
Apr. 10	5,479	6,410	--------	931	116.99	--------	--------	100	19.5	67.10	31	87.80
11	5,609	5,289	320	--------	94.29	--------	--------	63	19.5	67.10	27	80.60
12	6,052	6,183	--------	131	102.16	--------	--------	85	13.25	55.85	20.5	58.90
14	5,150	4,672	478	--------	90.72	--------	--------	7	15	59	19	66.20
15	5,825	5,662	163	--------	97.20	--------	--------	91	14.5	58.10	17.5	63.50
16	9,757	8,537	1,220	--------	87.50	--------	--------	100	7.25	45.05	22	71.60
17	8,318	7,940	378	--------	95.46	--------	--------	5	14	57.20	21	69.80
18	6,086	5,943	143	--------	97.65	--------	--------	10	15.5	59.90	21	69.80
19	17	15	2	--------	88.24	--------	--------	0	7.5	45.50	10	50
20	2,465	2,489	--------	24	100.97	−190	--------	100	7	44.60	15	59
21	34	30	4	--------	88.24	--------	--------	18	3	37.40	10	50
22	7,439	6,822	617	--------	91.71	--------	--------	100	0.5	32.90	14	57.20
23	2,262	1,955	307	--------	86.43	−180	--------	78	4	39.20	14	57.20
24	11,288	10,847	441	--------	96.09	−410	--------	100	1.5	34.70	17	62.60
27	12,501	10,557	1,944	--------	84.44	−480	--------	41	13	55.40	30	68
28	14,340	12,005	2,335	--------	83.72	−370	--------	52	7	44.60	17	63.60
29	15,964	20,404	--------	4,440	127.81	−430	--------	95	3	37.40	19	66.20
30	20,023	16,558	3,465	--------	82.69	−200	--------	100	8.5	47.30	22	71.60
May 1	19,941	20,063	--------	122	100.61	−320	--------	100	8.5	47.30	22	71.60
2	26,475	26,099	376	--------	98.58	−150	--------	94	11	51.80	27	80.60
3	11,389	10,288	1,101	--------	90.33	110	--------	6	16	60.80	20	68
7	31,926	31,185	741	--------	97.68	−150	--------	94	18	64.40	28	82.40
8	33,253	33,687	--------	434	101.31	320	9.5	100	15	59	25	77
9	39,765	39,313	452	--------	98.86	500	12.7	80	12	53.60	24.5	76.10
11	55,231	59,658	--------	4,427	108.02	1,440	24.1	100	16	60.80	30	86
12	44,931	48,875	--------	3,944	108.78	490	10.0	46	17	62.60	24	75.20
13	50,869	58,887	--------	8,018	115.76	940	15.9	64	16	60.80	26	78.80
15	54,061	54,528	--------	467	100.86	850	15.6	76	14	57.20	25	77
16	67,863	60,377	7,486	--------	88.97	870	14.4	87	11	51.80	28.5	83.30
17	22,992	23,218	--------	226	100.98	220	9.5	0	14	57.20	20	68
18	29,247	30,478	--------	1,231	104.21	--------	--------	0	18	64.40	20.75	69.35
19	65,407	66,898	--------	1,491	102.28	--------	--------	84	15	59	23.25	73.85
20	71,008	66,844	4,164	--------	94.14	1,170	17.5	68	10	50	25.5	77.90
21	61,438	56,135	5,303	--------	91.37	920	16.4	75	14	57.20	29	84.20
22	49,078	44,597	4,481	--------	90.87	1,130	25.3	79	17	62.60	30	86
23	51,854	48,268	3,586	--------	93.08	890	18.4	88	15.5	59.90	30	86
24	65,259	63,395	1,864	--------	97.14	560	8.8	99	15	59	28	82.40
26	42,138	38,356	3,782	--------	91.02	130	3.4	23	19	66.20	26	78.80
27	10,588	10,030	558	--------	94.73	−330	--------	6	14	57.20	21.5	70.70
28	47,397	42,663	4,734	--------	90.01	100	2.3	94	17	62.60	23	73.40
29	51,640	49,338	2,302	--------	95.54	−200	--------	99	8.5	47.30	26	78.80
30	52,987	49,534	3,453	--------	93.48	−130	--------	100	13	55.40	27	80.60
31	49,474	50,580	--------	1,106	102.24	−80	--------	70	13	55.40	27	80.60
June 1	44,882	45,693	--------	811	101.81	--------	--------	0	17	62.60	24	75.20
2	30,852	28,499	2,353	--------	92.37	--------	--------	14	20	68	26	78.80
4	58,564	56,128	2,436	--------	95.84	−290	--------	77	16.5	61.70	30	86
5	28,432	29,830	--------	1,398	104.92	--------	--------	3	19	66.20	24	75.20
6	54,772	53,883	889	--------	98.38	−50	--------	59	20	68	31	87.80
8	51,531	49,607	1,924	--------	96.27	60	1.2	54	19	66.20	31.5	88.70
9	55,678	52,066	3,612	--------	93.51	−120	--------	45	21	69.80	28	82.40
11	48,043	50,524	--------	2,481	105.16	−90	--------	81	22	71.60	31.5	88.70
12	39,231	39,915	--------	684	101.74	--------	--------	97	20.5	68.90	28	82.40
13	30,423	29,266	1,157	--------	96.20	--------	--------	66	10	50	22	71.60
14	3,399	3,501	--------	102	103.00	--------	--------	0	17	62.60	18	64.40
21	17,980	20,447	--------	2,467	113.72	−20	--------	54	18	64.40	29	84.20
22	25,654	26,617	--------	963	103.75	−340	--------	94	17	62.60	24.5	76.10
23	41,361	37,244	4,117	--------	90.05	−610	--------	91	15	59	28.5	83.30
24	39,667	36,505	3,162	--------	92.03	−110	--------	81	12	53.60	31.5	88.70
25	45,182	42,060	3,122	--------	93.09	−160	--------	96	18.5	65.30	32.5	90.50
26	35,789	31,046	4,743	--------	86.75	−30	--------	74	18	64.40	29.5	85.10
29	32,173	25,941	6,232	--------	80.63	−300	--------	61	20.5	68.90	29	84.20
30	34,974	28,807	6,167	--------	82.37	−380	--------	98	19	66.20	33	91.40
July 1	37,834	30,626	7,208	--------	80.95	−110	--------	64	23	73.40	34	93.20
2	38,339	29,880	8,459	--------	77.94	--------	--------	64	20	68	35	95

[1] The hive was not on scales for the first few days of observation. On some later days an accumulation of moisture on the tops and on the bottom-board introduced erroneous records of weight, and such days have been omitted from this table.

[2] Figures in this column indicate the minimum limit of the average loads for the day and not the actual average load. Since consumption of stores and evaporation continue throughout the day, the actual average load can not be obtained from weights of the entire hive. This limit can only be determined for those days when the hive showed a gain due to incoming nectar.

TABLE 1.—*A seasonal survey of some observations for entire days*—Con.

Date	Total exits	Total returns	Loss	Gain	Per cent returns are of exits	Loss or gain in weight of hive	Average load per returning bee	Per cent of possible sunshine	Temperature in shade during period of observations			
									Minimum		Maximum	
						Grams	*Milligrams*		*° C.*	*° F.*	*° C.*	*° F.*
July 3---	28, 918	24, 074	4, 844	-------	83. 25	−100	-------	53	22	71. 60	32. 5	90. 50
4---	3, 206	2, 506	700	-------	78. 17	-------	-------	0	19	66. 20	22	71. 60
5---	16, 384	14, 404	1, 980	-------	87. 92	−410	-------	24	15	59	25	77
6---	23, 954	22, 635	1, 319	-------	94. 49	−360	-------	94	13. 5	56. 30	28	82. 40
8---	15, 267	14, 737	530	-------	96. 53	-------	-------	57	20	68	31. 5	88. 70
9---	19, 897	20, 003	-------	106	100. 53	−150	-------	82	20. 5	68. 90	31. 5	88. 70
10---	17, 619	17, 305	314	-------	98. 22	−180	-------	72	21	69. 80	29	84. 20
11---	22, 973	21, 784	1, 189	-------	94. 82	−80	-------	59	21. 5	70. 70	31	87. 80
12---	19, 509	20, 281	-------	772	103. 96	−320	-------	100	23. 5	74. 30	35	95
13---	17, 947	17, 931	16	-------	99. 91	-------	-------	68	23	73. 40	34	93. 20
14---	3, 302	3, 148	154	-------	95. 34	−170	-------	0	19. 5	67. 10	23	73. 40
15---	14, 976	16, 182	-------	1, 206	108. 05	−220	-------	46	18	64. 40	29	84. 20
16---	17, 935	18, 968	-------	1, 033	105. 76	000	-------	53	19. 5	67. 10	28	82. 40
17---	13, 284	14, 808	-------	1, 524	111. 47	-------	-------	71	20	68	33	91. 40
18---	14, 372	14, 498	-------	126	100. 88	-------	-------	58	20. 5	68. 90	34. 25	93. 65
19---	21, 502	21, 828	-------	326	101. 52	−340	-------	35	21. 5	70. 70	31	87. 80
20---	8, 956	9, 131	-------	175	101. 95	−330	-------	6	20	68	25. 5	77. 90
21---	20, 916	21, 535	-------	619	102. 96	−340	-------	100	15	59	30	86
22---	18, 376	19, 389	-------	1, 013	105. 51	-------	-------	66	21	69. 80	30	86
23---	23, 881	24, 974	-------	1, 093	104. 58	−370	-------	85	19	66. 20	32	89. 60
24---	17, 460	18, 006	-------	546	103. 13	−240	-------	85	22	71. 60	32. 25	90. 05
25---	10, 079	10, 087	-------	8	100. 08	-------	-------	31	20	68	29	84. 20
26---	3, 687	3, 963	-------	276	107. 49	−70	-------	3	19	66. 20	24	75. 20
27---	12, 003	13, 054	-------	1, 051	108. 76	−120	-------	49	20	68	28	82. 40
29---	8, 683	8, 861	-------	178	102. 05	−250	-------	80	15	59	29. 5	85. 10
Total----	2,434,666	2,357,769	-------	-------	-------	-------	-------	-------	-------	-------	-------	-------

Throughout the honey flow and for the next five weeks after its close, the total daily exits show a gradual falling off, until the sixth week, when there is a rather sudden falling off from 40,000 to a number fairly constant for a period throughout July, during which the total number of possible daily exits is about one-third of those occurring on the best days in the honey flow in May. This indicates that the emergence of young bees is not sufficient to replace the high death rate following the honey flow, until the majority of these old bees have died off. There is, of course, every gradation in flight from the best days in the honey flow to other days on which practically no flights take place.

It is noticed that on heavily overcast days, with or without occasional precipitation, the low intensity of light seems to be the strongest factor inducing the bees to stay at home. Days that are bright and sunny, but ushered in by a low morning temperature, show some remarkable differences in the totals for the day, amounting in certain cases to as much as 40 to 50 per cent of the possible flight for the period. For each day throughout the season that does not come up to the optimum flight curve, some factor or group of factors has been at play, modifying the flights to a less or greater degree. Such data, however, do more than substantiate the well-known facts concerning bee behavior indicated above, for they also give a means of measuring the exact influence of any factor or group of factors.

INFLUENCE OF STORMS AND RAIN

The period of the season of 1922 in which these data were obtained included many bright days on which storms occurred during the course of the afternoon, giving an excellent opportunity to study the behavior of the bees on the approach of a storm; in fact, for the purposes of a brief general study of flight activities, there were too many such days.

The influence of a storm is well shown by the data for a single day (Table 3, and fig 4.) The records on which this curve is based were taken on May 15, a bright, sunny day until the afternoon. The following chronological data show the weather conditions:

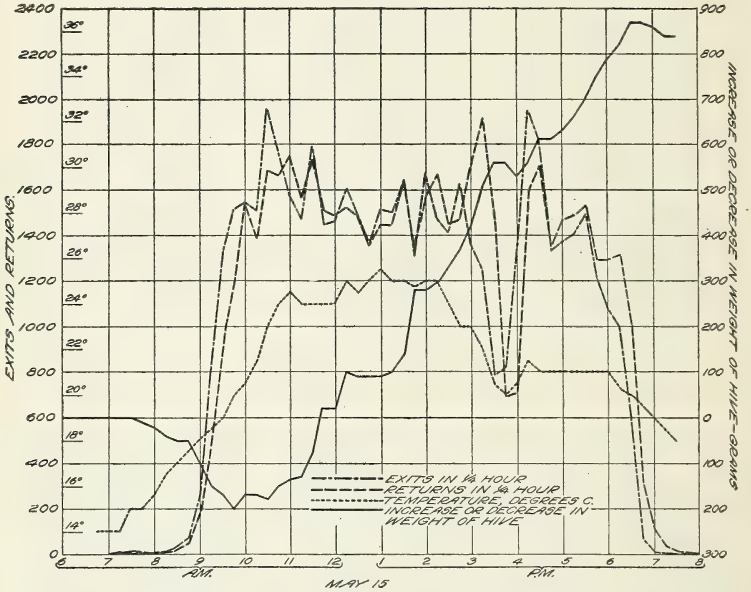

FIG. 4.—Flight, temperature and hive-weight data for May 15, 1922, showing the effect of a threatened storm (2.30–4.15 p. m.) on flights

Time	Weather conditions
2.30	A clouding over is noticed.
2.45	The very much darkened sky indicates the sudden approach of a storm.
3.00	It is thundering, and an increase in the number of heavily laden nectar-carrying bees is noted at the gates.
3.15	A gusty wind is blowing, precipitation being expected any minute.
3.30	The storm is passing from a westerly direction to a southerly. The very dark nucleus of the storm, where precipitation appears to be taking place, is from 3 to 4 miles away.
3.45	The air is calmer, the storm having passed without any precipitation.
4.00	The sun is shining occasionally and for short intervals.
4.15	The sun is shining steadily, and it has cleared up completely. [This condition continued for the remainder of the day.]

No better example of the sudden approach of a storm with all its symptoms to the very point of precipitation, but without actual precipitation, could have been obtained.

TABLE 2.—*Length of bees' flights in minutes per trip to and from the hive*

Date	Period of day's flights	Length of period	Flights during period		Number of times flight was ascertained	Average number in field flights	Probable error of average in round numbers (±)	Probable error of average expressed in per cent of average (±)	Average duration of trips	
			Exits	Returns					Based on exits	Based on returns
		Minutes							*Minutes*	*Minutes*
Apr. 15	2.00- 5.00	180	2,597	2,572	4	148	9	6.21	10.26	10.36
20	12.30- 2.00	90	1,100	1,130	4	112	8	7.26	9.16	8.92
May 8	11.30- 4.30	300	16,761	16,801	11	1,974	9	.46	35.33	35.25
9	11.00- 6.00	420	29,176	29,200	23	2,980	54	1.83	42.90	42.86
15	9.45- 3.00	315	32,492	32,265	22	1,567	28	1.78	15.19	15.30
15	4.15- 5.15	60	5,920	6,023	5	1,148	17	1.49	11.63	11.43
17	12.30- 2.30	120	6,408	6,678	9	776	27	3.50	14.53	13.94
20	12.00- 2.00	120	10,908	10,006	9	2,654	30	1.12	[1] 29.19	[1] 31.83
22	10.30-12.45	135	[1] 9,588	8,973	10	2,713	41	1.52	[1] 38.19	[1] 40.80
June 1	8.15- 2.15	360	29,687	29,322	25	1,732	66	3.83	21.00	21.26
6	9.00-11.00	120	11,658	11,027	9	3,283	74	2.25	[1] 33.79	[1] 35 73
6	11.15-12.00	45	4,299	3,117	4	4,321	167	3.88	[1] 45.23	[1] 62.38
6	12.15- 4.00	225	20,094	19,934	16	5,674	41	0.73	[1] 63.52	[1] 64.03
12	8.00- 9.30	90	4,553	3,257	7	1,817	116	6.38	35.90	50.18
12	9.45- 4.45	420	28,303	28,422	29	3,683	46	1.25	54.64	54.41
25	10.30-12.45	135	[1] 9,128	9,167	10	4,170	21	0.51	61.66	61.40
July 9	10.30- 3.30	300	11,103	11,314	21	3,571	37	1.04	96.49	94.69
10	10.45- 3.30	285	9,166	9,064	20	3,305	31	0.94	102.73	103.92
12	9.15- 3.00	345	13,158	13,442	24	1,941	79	4.06	50.89	49.81
13	9.30- 2.30	300	11,087	10,873	21	2,389	32	1.33	64.64	65.91
18	9.15-12.30	195	7,931	8,190	14	1,654	48	2.91	39.53	39.28
18	3.15- 4.45	90	638	637	7	138	4	2.70	19.47	19.49
24	9.00- 3.00	360	10,397	10,481	25	719	20	2.77	24.89	24.69
25	9.00-10.15	75	1,501	1,512	5	534	9	1.73	26.63	26.44
25	10.45- 2.15	210	4,581	4,405	15	980	20	2.01	44.88	46.67
25	11.30-12.00	30	851	847	3	1,072	7	0.70	37.79	37.97
25	12.15- 1.00	45	898	731	4	866	32	3.69	43.39	53.31
25	1.15- 2.15	60	1,274	1,280	5	1,070	9	0.86	50.39	50.16
29	9.45- 3.45	360	5,822	6,357	25	505	12	2.42	31.23	28.60

[1] Correction applied for bees registered as lost.

TABLE 3.—*Record of exits and returns, total and per quarter hour, and of bees in the field, May 15, 1922*

Time	Total exits	Total returns	Bees in field	Exits in one-quarter hour	Returns in one-quarter hour
			Number	*Number*	*Number*
7.00	0	0	0	0	0
7.15	7	0	0	7	0
7.30	7	15	−8	0	15
7.45	9	26	−17	2	11
8.00	12	31	−19	3	5
8.15	19	43	−24	7	12
8.30	43	59	−16	24	16
8.45	110	108	2	67	49
9.00	367	280	87	257	172
9.15	1,225	798	427	858	518
9.30	2,557	1,727	830	1,332	929
9.45	4,075	2,897	1,178	1,518	1,170
10.00	5,621	4,448	1,173	1,546	1,551
10.15	7,131	5,834	1,297	1,510	1,386
10.30	9,091	7,526	1,565	1,960	1,692
10.45	10,864	9,187	1,677	1,773	1,661
11.00	12,437	10,939	1,498	1,573	1,752
11.15	13,905	12,508	1,397	1,468	1,569
11.30	15,696	14,246	1,450	1,791	1,738
11.45	17,138	15,560	1,578	1,442	1,314
12.00	18,597	17,046	1,551	1,459	1,486
12.15	20,200	18,577	1,623	1,603	1,531
12.30	21,686	20,065	1,621	1,486	1,488
12.45	23,063	21,423	1,640	1,377	1,358
1.00	24,577	22,867	1,710	1,514	1,444
1.15	26,086	24,310	1,776	1,509	1,443
1.30	27,731	25,951	1,780	1,645	1,641
1.45	29,042	27,289	1,753	1,311	1,338
2.00	30,708	28,865	1,843	1,666	1,576
2.15	32,181	30,541	1,640	1,473	1,676
2.30	33,595	31,989	1,606	1,414	1,448
2.45	35,223	33,457	1,766	1,628	1,468
3.00	36,567	35,162	1,405	1,344	1,705
3.15	37,807	37,077	730	1,240	1,915
3.30	38,590	38,577	13	783	1,500
3.45	39,410	39,270	140	820	693
4.00	40,740	39,979	761	1,330	709
4.15	42,688	41,575	1,113	1,948	1,596
4.30	44,500	43,278	1,222	1,812	1,703
4.45	45,830	44,634	1,196	1,330	1,356
5.00	47,204	46,105	1,099	1,374	1,471
5.15	48,608	47,598	1,010	1,404	1,493
5.30	50,105	49,132	973	1,497	1,534
5.45	51,315	50,421	894	1,210	1,289
6.00	52,394	51,718	676	1,079	1,297
6.15	53,392	53,035	357	998	1,317
6.30	53,987	54,052	−65	595	1,017
6.45	54,048	54,366	−318	61	314
7.00	54,058	54,474	−416	10	108
7.15	54,061	54,513	−452	3	39
7.30	54,061	54,528	−467	0	15

It is noticed that the bees did not respond to the cloudiness at 2.30 p. m.; but when the sky darkened at 2.45 p. m. the curve representing incoming bees immediately began its rapid ascent and the outgoing bees showed a decrease, the divergence of the two curves continuing at an equal rate until 3.15 p. m., when the greatest number of returning bees had entered the hive. The climax of the threatening storm was just previous to 3.30 p. m., when the curve of outgoing bees reached its lowest point, and all but 13 of the bees in the field had entered the hive. At this point the surprising fact is revealed by this day's record that, although the storm was so severe as momentarily to send all the field bees back to the hive, the impulse of the bees to go to the field while the secretion was good was so strong that in the half hour in which the climax of the threatening storm occurred as many as 50 to 75 per cent of the bees, which were going out under optimum conditions for this day, were still leaving the hive. The quick response of the bees, this time to the gradual but rapidly improving conditions of the weather, is seen from 3.30 to 4.15 p. m., when normal activity was resumed. It is interesting to speculate as to just what feature of the storm contributed most to this behavior in the flight of the colony. Was it drop in temperature, variation in light or atmospheric pressure, difference in humidity, intensity of the wind, or general change in the electrical conditions of the atmosphere? Unfortunately, not all of these questions can be answered definitely as yet.

Of all these factors, temperature and light varied most. If temperature had been the chief cause, the flight might have been expected to remain low after the storm, since the temperature remained low for the remainder of the afternoon. The response to the change in light, both its increase and its decrease in intensity, can be so closely correlated with the flight activity that this may be safely considered the chief cause of the variation.

Comparing this day with May 13 (see Table 1), when the number of field bees was perhaps slightly less and on which there were 58,887 returns, we find that there were only 54,528 on May 15, which shows that the threatening storm of the latter day reduced the total flights by at least 7.40 per cent. On the assumption that the nectar conditions on these two days were identical, this represents a loss of 69.58 grams, due to this clouding over. Actually 90 grams less nectar was gathered, which would indicate that there was little or no difference in the nectar conditions on these two days.

Comparing May 15 with May 16, which was bright and sunny all day, with 60,377 returns, it is found that the decrease in total flight on May 15, apparently due to this storm, was 9.69 per cent. Only 20 grams more nectar was gathered on the 16th, showing that although a good day it was not quite so good a day for nectar secretion as either May 13 or May 15. This indicates that the afternoon storm of May 15 reduced the day's flight by from 7.40 to 9.69 per cent with, of course, a corresponding reduction in the day's gathering compared with an optimum secretion.

The record of July 8 (fig. 5) is typical of the flight when actual precipitation occurs. This was a bright, sunny day until 12.30 p. m., when a general clouding over occurred. The following data show the progress of this storm:

Time	Weather conditions
1.00	A few drops are falling.
1.15	The sprinkling has ceased.
1.30	Thundering, sky very dark, beginning to rain gently.
1.45	Light rain falling.
2.00	Raining heavily.
2.30	The rain has stopped.
4.30	The sky has cleared, but the sun is obstructed by some clouds.
5.00	The sun is shining brightly.
6.00	The sky is again clouded. [This condition persisted until dusk.]

This was in a period of the year when, on account of the scarcity of nectar, a relatively larger percentage of the field bees are absent from the hive at any particular time. On the approach of a storm, therefore, their homeward rush produces a much higher peak, relative to the normal trend of the curve, than would occur if nectar were abundant. On this day on the approach of the storm in the quarter hour ending at 1 p. m., three times as many bees returned as in the highest quarter-hourly return preceding the storm. A slight flight from the hive was apparent even through the light rain; but when at 2 p. m. the heavy rain began, the exits were reduced to about a sixth of those in the morning when the sun was shining brightly. Though the sun again shone brightly between 5 and 6 p. m., and the temperature was high, this low flight activity still persisted, indicating that in some way the bees seemed to know that any further effort would not be profitable, a behavior differing markedly from that of May 15, when the response to good weather by increased flight was immediate.

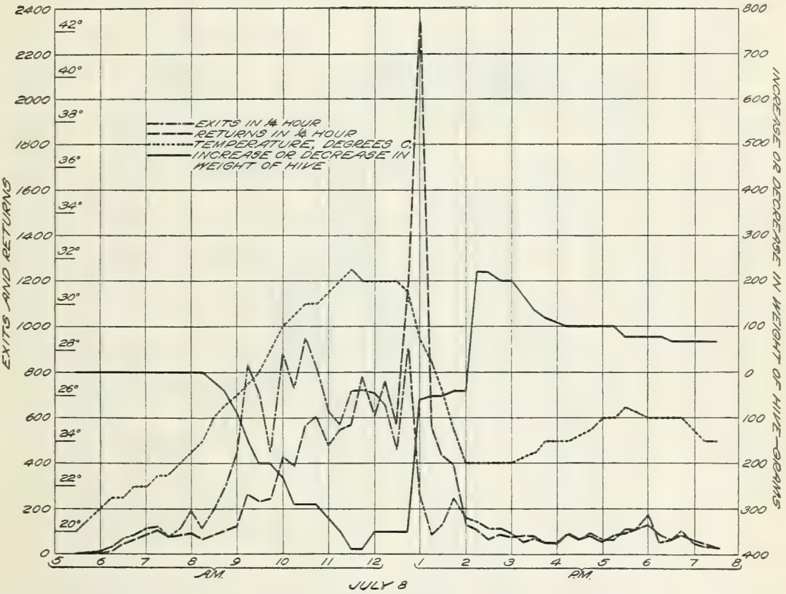

FIG. 5.—Flight, temperature, and hive-weight data for July 8, 1922, showing the effect of a storm (1.30–2.30 p. m.) on flights

After such storms have cleared, it has been noted that a few of the returning bees show by the matted-down appearance of the hairs of their bodies that they have been caught in the storm and after drying have flown back to the hive.

Showers, if they are of sufficient strength, produce the same effect as a severe storm, the periodicity of the curve corresponding exactly with the time of each shower. The effect of a shower of rain lasting only from 5 to 10 minutes is well illustrated by the records for May 19 (fig. 6), where a marked depression in the two curves is produced, the record of the weight of the hive showing a sudden increase during the shower, to be followed immediately by an equally abrupt decrease on the resumption of clear weather.

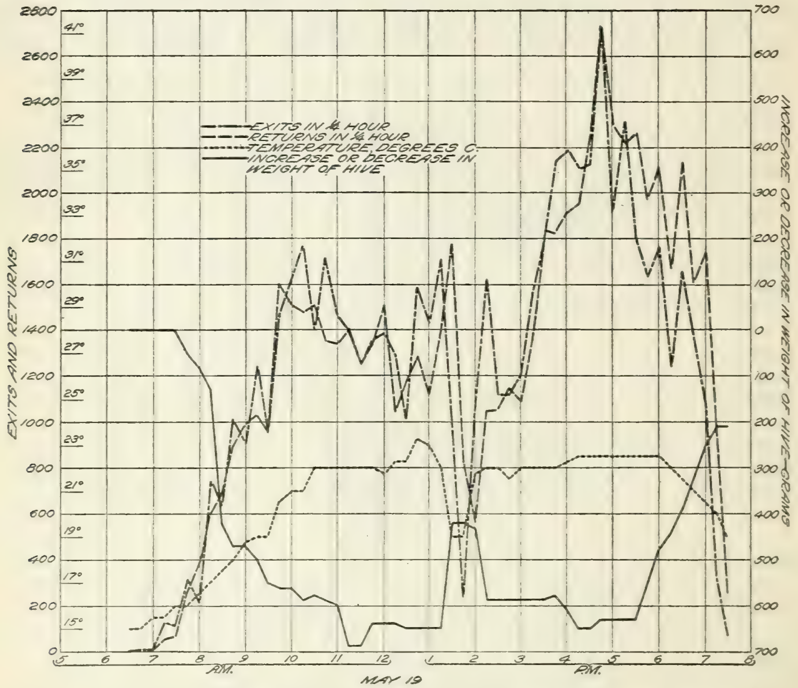

FIG. 6.—Flight, temperature, and hive-weight data for May 19, 1922, showing the effect of a shower of short duration on flights

The flight on an overcast day with some rain is illustrated by that of May 18 (fig. 7). The day set in dull with the following weather records:

Time	Weather conditions
6.00 to 9.15	Heavily overcast. At 6.30 a shower of short duration occurred.
9.15 to 10.15	Sprinkling.
10.15 to 11.00	Light rain.
11.00 to 11.45	Sprinkling.
11.45 to 12.15	Steady rain.
12.15 to 1.00	Heavy rain.
1.00 to 1.30	Light, steady rain.
1.30 to 2.00	Sprinkling.
2.00 to 2.15	It has stopped sprinkling.
2.15 to 2.45	Brighter, though still overcast, light frequently varying in intensity.
2.45 to 3.00	Becoming darker again.
3.00 to 3.15	Heavily overcast.

3.15 to 3.45 A few drops are falling.
3.45 to 4.00 Sprinkling.
4.00 to 4.30 Steady shower falling.
4.30 to 4.45 Sun shining brightly, though shower continues.
5.00 Rain has stopped, bright sunshine.
5.15 Again clouding over.
5.45 A few drops falling.
6.00 The sun is shining through the clouds for brief intervals.

Although this day occurred between others of good honey flow, the hive showed a loss in weight. An apparent gain in early afternoon was due to water on the hive. Each period of rain caused a decrease in flight, the heavy rain about noon causing the greatest decrease. In each case the bees resumed flight promptly with the slightest improvement of weather conditions.

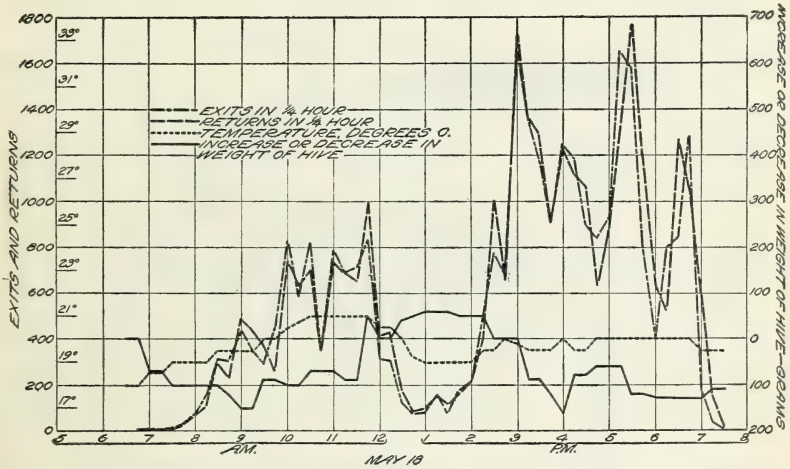

FIG. 7.—Flight, temperature, and hive-weight data for May 18, 1922, showing the effect on flight of an overcast day with occasional showers

THE EFFECT OF WIND

Unfortunately for a thorough study of the effect of wind, there were few days during the period of these observations when the wind was strong enough to affect the flight appreciably. The information is drawn from the records of only five days, and such statements as can be made on this subject are therefore made with some reservation.

April 11 was a windy day, with no substantial honey flow. The successive numbers of exits increased with the rise in temperature until 8.30 a. m. During this period the velocity of the wind was only 4 to 5 miles per hour. Between 8.30 and 9 a. m. the wind velocity reached 10 miles per hour and the flight dropped and continued low, while the velocity of the wind increased to 11 and 15 miles per hour. At 2 p. m. the velocity fell to 6 miles per hour and later to 4 miles, with the flight responding by an increase, which no other observed factors would explain.

This record might suggest that a velocity of 10 miles per hour is the minimum velocity appreciably affecting flight. However, this can not be the case, for on April 10 a play flight took place, when the wind velocity was as high as 14 to 17 miles per hour. Again, on May 19 (fig. 6), a day when the morning's weight was all but regained at the end of the day, a wind of 9 to 10 miles per hour, from 8 a. m. to 4 p. m., apparently scarcely affected the flight, which was greater by 54 returns than on the following day when the wind velocity was only 1 to 4 miles per hour. On these two days the wind velocity was taken from an anemometer about 5 feet from the ground and about 20 feet from the hive.

The only other windy day of any consequence—June 22, a day in the dearth—during which from 9 a. m. to 6 p. m. the wind varied from 16 to 21 miles per hour shows a reduction of 28.53 per cent in the total day's flight, when compared with June 23, a day with little or no wind. The wind velocity on the former day is taken from the data obtained by the Weather Bureau in Washington at a higher elevation from the ground.

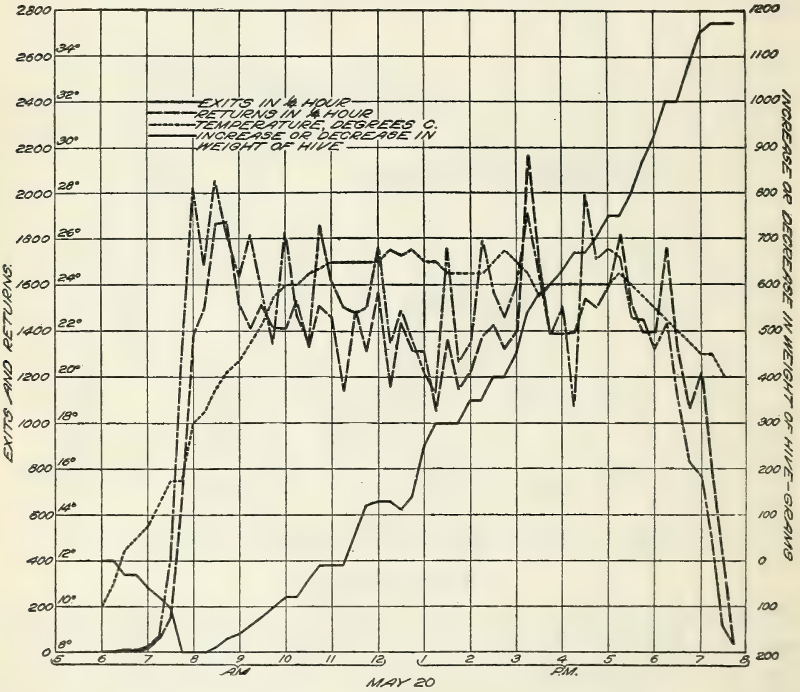

FIG. 8.—Flight, temperature, and hive-weight data for May 20, 1922, a day in a time of honey flow

THE EFFECT OF TEMPERATURE

It is only when all the factors influencing flight but one are at least at an intensity favorable for flight, and this last factor is increasing in intensity toward this condition, that its minimum intensity can be determined. Any one factor can become the lagging factor at one time or another. In the early part of the season temperature is this factor more often than any other.

To present all the data from which the following conclusions on the effect of temperature have been reached would unduly increase the volume of this paper. Such as are essential have been inserted in the curves for the flights of May 15 (fig. 4), May 19 (fig. 6), May 20 (fig. 8), July 8 (fig. 5), July 10 (fig. 9), and July 12 (fig. 10); and these curves have been presented mainly to illustrate phases of behavior other than the responses of bees to temperature.

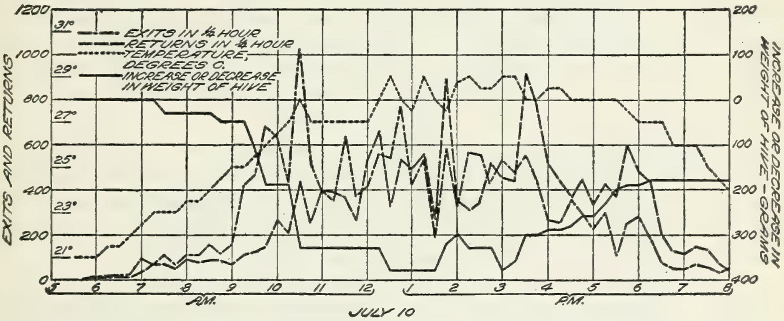

FIG. 9.—Flight, temperature, and hive-weight data for July 10, 1922, a day in a time of dearth

A study of the temperature at which flight commenced on each of the successive days of this investigation shows:

1. Under a particular set of conditions this temperature is uniformly within 2° to 3° C. of a certain definite temperature, which however, is not the same throughout the season. During April flight usually began between 12° and 14° C. (53.6° and 57.2° F.). In May the temperature at which the first bees came out was usually from 14° to 16° C. (57.2° to 60.8° F.), with the main flight beginning at 16° or 18° C. (60.8° or 64.4° F.). In June and July the temperature at which flight commenced was very inconstant, varying between 13° C. (55.4° F.) and 27° C. (80.6° F.), being most frequently from 19° to 25° C. (66.2° to 77° F.), and showing that at this time of the year temperature is not often a factor in retarding the beginning of flight.

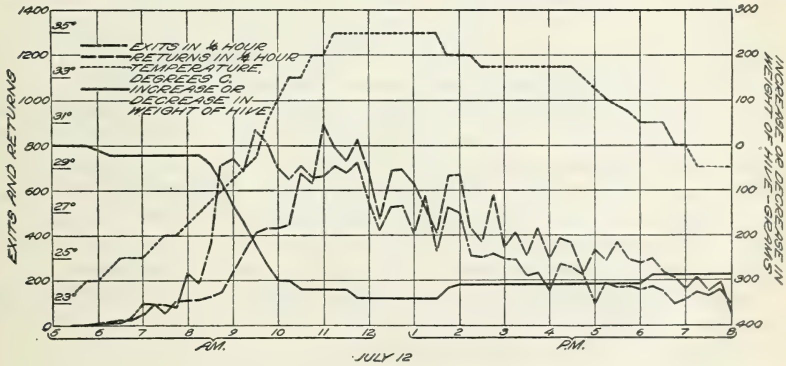

FIG. 10.—Flight, temperature, and hive-weight data for July 12, 1922, a day in a time of dearth

2. On dull, overcast days the bees usually do not begin their flight until the temperature has risen at least 2° C. (3.6° F.) higher than the usual temperature for beginning flight for that period. This was very marked in April, May, and the early part of June, but was not so obvious during the latter part of June and the month of July.

3. The internal condition of the colony is important in determining the temperature at which flight will begin. Colonies in the apiary that were stronger than the one under experimentation always commenced their flight at somewhat lower temperatures. The lowest temperature at which the flights from this colony began was on two days in April, when the temperature was as low as 10° C. (50° F.).

4. No marked difference in flight temperature between honey flow and dearth conditions in the same period can be found, and no conclusive evidence has been observed from these data that a heavy honey flow induces the bees to go out in large numbers at a temperature lower than they would if no nectar were available.

5. If from a lower temperature the thermometer rises rapidly to a condition suitable for flight, the temperature at which flight commences is usually 2° C. or more higher than if the temperature had risen slowly. In the first case, the flight curve usually shows a more gradual ascent to its peak; in the latter, a more rapid rise is observed, indicating, as might be expected, that the hive as a whole must absorb a certain amount of heat before the bees become active enough for a general flight.

6. A comparison of the temperature at which the flight begins its upward trend and that at which it begins its descent in the afternoon shows that, without exception, the temperature at which the bees begin to slacken their flight activities in the afternoon is higher than that at which they become active in the morning, the difference ranging from 1° to 9° C. This indicates that it is the waning light which accompanies the approach of sunset, rather than a fall in temperature at that time, that causes the decrease in flight.

7. A study of the seasonal flight curve (fig. 2) shows that a low morning temperature, by postponing the time at which flight commences, may reduce the total possible daily exits by as much as 50 or even 75 per cent. Days which appear to be similar in every other respect, but on which a variation in flight of from 10 to 25 per cent is noted, furnish records which show that this difference may be traced to lower temperatures in the early part of the day.

8. On some excessively hot days the flight curves remained low. Whether this behavior is due to the high temperature or to the dearth existing it is impossible to say.

THE EFFECT OF LIGHT

Since temperature and light intensity are so closely correlated, it is exceedingly difficult to differentiate the behavior produced by variations in either of these factors. In the study of the effect of light, a record was made of the degree of cloudiness each quarter of an hour while flight was occurring. Because of variations in the density, altitude, and position of the clouds, to say nothing of the personal equation in the taking of such intangible data, this method was not wholly satisfactory, though useful for a broad interpretation. A better method would have been to supplement these data with an actual measurement of the light intensity by means of a photometer. Had this been done, when light is a lagging factor a more definite intensity would have been found marking the commencement of flight and on the approach of sunset the intensity at which the number of exits begins to fall would also prove to be rather definite. Whether these two intensities as affecting flight at the beginning and end of the day would be identical, or whether the evening intensity is lower or higher than the morning is a matter yet to be determined.

The flight curve typical of a bright, sunny day with all other factors at their most favorable intensity shows a sudden ascent to a point where the outgoing and incoming bees begin to balance in number, and continues more or less level till, at the end of the day's flight, the descent of the curve is as abrupt as was its commencement.

On dull days the ascent of the curve is more gradual, as is usual when some factor is not at an optimum.

Comparing the months of May and July, it is found that on the first day of May the sun rose at 5.03 and on the last day at 4.37 a. m. Although the flight commenced about 7 a. m. on most of the sunny days in this month, the first quarter of an hour having exits amounting to at least 400 bees ended at 7.45 or 8 a. m. Throughout July, on the other hand, when the sun rose about the same time (4.38 to 4.59 a. m.), on account of the high temperature prevailing the first bees were flying as early as 5.45 to 6 a. m. and yet the first quarter of an hour with as many as 400 exits usually did not occur until 8.15 to 8.45 a. m. Though the colony was weaker in July than in May, these facts reflect the nectar conditions prevailing rather than the effects of temperature or light.

THE HONEY FLOW

A survey of the flight activities of the season as a whole (fig. 2 or Table 1) shows that of all the external environmental factors which influence the magnitude of the flight occurring on any normal day, a heavy honey flow of nectar is the strongest. These flights during the honey flow (May 3 to May 28) were on the average three to four times as great as at any other period of the observations (see fig. 2). In order to follow in minute detail the variations in the flight which occur in the course of a day's activity, the number of bees departing and the number returning to the hive each quarter of an hour have been recorded, as well as the quarter-hourly change in the weight of the hive.

The flights typical of the honey flow are well illustrated by the records for May 20 (fig. 8) or May 15 (fig. 4), and those of a dearth are also well illustrated by the records of July 10 (fig. 9), July 12 (fig. 10), and May 19 (fig. 6), a day of dearth within the period of the honey flow. In general it is found that at the beginning of the day's flight the number of bees leaving each quarter of an hour becomes larger and larger, to be followed later by a corresponding increase, as on May 20 (fig. 8) or July 12 (fig. 10), in the number of bees returning. At the close of the day's flight the successive numbers of outgoing bees decrease, followed later by a corresponding decrease in the number of returns until flight ceases for the day.

The characteristic differences typical of the flights during a honey flow and dearth are respectively:

1. During the honey flow, as on May 20 (fig. 8), there is a very steep ascent of the outgoing curve on the advent of the optimum conditions for flight, with a corresponding abrupt descent in the curve on the approach of sundown. In a dearth, as on May 19 (fig. 6) or July 12 (fig. 10), these ascents are more gradual. Instead of the peak of the flight being reached within three-quarters of an hour or an hour after the main flight to the field begins, as in the honey flow, it is not attained until about four or even five hours later.

2. In the honey flow the portion of the curve lying between the morning peak and the time when, at the close of flight, the number of exits begins to drop, approximates a horizontal straight line, showing that the rate of flight is fairly constant, there being almost as many bees departing as arriving. In the dearth, on the other hand, as on July 12 (fig. 10), this portion of the curve is not horizontal but tapers away gradually to zero, indicating that on the discovery of the dearth the bees conserve their energies by reduced activity.

3. The horizontal distance (indicating length of flight) between the curves representing the outgoing and incoming bees in a heavy honey flow is always shorter and sometimes very much shorter than it is in a dearth. This is specially apparent when in the morning the flights are on the increase and again in the evening when they are on the decrease. This distance, which is indicative of the average duration of each voyage, can not be followed precisely on a curve plotted in this manner. This will be dealt with separately in a discussion of the average duration of the trips (p. 26).

4. A study of the changes in weight of the hive, indicated in Figures 4 to 10, shows that as the successive number of departing bees increases the weight correspondingly decreases; then, again, as the number of nectar-laden returning bees increases the hive begins to regain its early morning weight. During the first days of the honey flow the time at which this regaining of the original weight occurs is well on in the afternoon or even at the end of the day. As nectar conditions improve, the time at which the original weight is regained comes earlier in the day. Then, as the honey flow wanes, this time again occurs toward the latter part of the day. In the dearth proper the drop in weight of the hive is considerable. This is due more to the long trips, with the majority of the flying force absent from the hive at one time, than to the small loads that they bring back. Since little or no nectar comes in, the morning weight is frequently never regained, a loss in weight being continually recorded for the entire day. This loss indicates the amount of stores consumed to maintain this flight activity in a main search for nectar, and to maintain other colony activity.

The amount of nectar gathered on any particular day depends not only upon the factors governing nectar secretion, but also on the factors governing the flights for that day. The secretion may be equally good on two selected days, but on account of a relatively adverse condition for flight of shorter or longer duration on one of these days the gathering may not be so great. A comparison of the amounts of nectar gathered on certain days is not always absolutely indicative of the amount of nectar available to the bees on these particular days. This will be seen clearly from an inspection of Table 1, in which are tabulated the total number of returning bees on each day (except when the weight records were disturbed by rain), the daily increase in weight of the hive, and the minimum limits of the average load carried by each bee on these respective days. The average load as given in this table is obtained by dividing the day's gain in weight by the total number of returns for the day. Since consumption of stores, evaporation of excess water in the nectar, and other sources of loss in weight of the hive as a whole are going on throughout the day, it is evident that the average loads here computed are actually the minimum limits for the average loads carried. Other observers have noted that bees sometimes carry larger loads of nectar than have been indicated for the best day, judging by the total gain of the colony for the day (May 11, 24.1 milligrams), so that the figures given in Table 1 are evidently very conservative. Throughout the following discussion the expression "average load" refers to these minimum limits. On May 15 slightly less nectar (20 grams) was gathered than on May 16, yet the average load was greater by 1.2 milligrams. The total day's gain was minimized by a threatening storm which reduced the number of possible flights.

Again, on May 22 the load per bee is high (25.3 milligrams), yet the total day's gathering is less than on May 20, when the average load was 17.5 milligrams. This can be accounted for only by the fact that on May 22 some factors were influencing the flights and lengthening the average duration of each flight by about 9 minutes (Table 2), which would in turn reduce the total exits for the day and the amount of nectar gathered.

Without a knowledge of the number of flights which occur, a study of the daily gains on May 9 and 24 would indicate that May 24 was a day of heavier secretion, since more nectar was brought in on this day; but a comparison of the total returns and the average load per bee shows that the reverse was the case.

In general, Table 1 shows that although there is a close relation between the average load carried by each bee and the daily total, the amount of nectar gathered is not necessarily indicative of the quantity of nectar available to the bees. The average load per bee is the true indicant.

On six days only—one in April, three in May, one in June, and one in July—did the frequency of the flights drop during the hours 12 m. to 2 p. m., as would be required by the weight curve described by Dufour (*1*) as typical of the spring conditions. On these days the drop did not last more than half an hour, and varied in magnitude from 15 to 40 per cent of the average number of exits or returns during the main flight for the day.

THE EFFECT OF HEAVY FLIGHT NEAR BY

Another colony about 36 feet from the one under experimentation was, on May 11, at 2.30 p. m., much disturbed by manipulation, so that the air in the vicinity was full of flying bees, almost as many as when a swarm is on the wing. When the curve for this day's record was plotted, an unusual peak, about 40 per cent higher than the normal trend of the curve, was noticeable at this time on both the ingoing and the outgoing curves. Although other peaks occur at different times, usually only on a single curve at one time, none was so marked as this particular one. If this peak was actually a response to this disturbance in the neighboring colony, it is interesting to speculate as to the method of conveyance of the information to the bees within the experimental colony. This question suggests another use for these instruments, namely, a study of the reaction of bees to odor, sound, and other external stimuli.

THE AVERAGE DURATION OF TRIPS

A study of the factors which influence the length of time the bees are absent from the hive on each foraging trip is a distinct problem in itself. The amount of nectar available in the flowers, the position and nature of the nectaries, and the distance which the bees must travel to obtain this nectar are the chief factors which govern the average duration of the voyages; therefore, an intimate knowledge of this duration and its variations is of importance in a study of nectar secretion, especially with reference to the time of day when the maximum secretion occurs. At present it is possible to give only a limited selection of data from different parts of the season to show the daily and seasonal variations in the duration of the trips which actually occurred in this experiment.

A simple graphic representation of the average duration of the trips and their variations in the course of a day is obtained by plotting the progressive totals of all the bees which have left the hive and of all those that have returned up to the time of each successive reading from the cyclometers. The plotting of the exits gives a continually ascending curve to the end of the day's flight. The plotting of the returns gives a curve which follows the first curve in time, as determined by the average duration of each trip for that period of the day's flight. The horizontal distance between the two curves represents the average time the bees spend in the field. The vertical distance between the two curves at any time of the day represents the number of bees in the field at that time.

If we suppose a purely hypothetical case, in which a constant number of bees leave the hive and return within a certain definite interval of time throughout the day, two parallel straight lines, representing the exits and returns, would be obtained when plotted as described above. By comparing two similar triangles on such a diagram it is found that the ratio of the number of bees (n) which return in a given interval of time (t), is to this time (t) as the number of bees in the field (f) is to the average duration of the trip (x); that is, $n:t::f:x$, or $x=\frac{tf}{n}$. Turning now, for example, to Table 3 (May 15, fig. 4) and Table 4 (July 10, fig. 9) it is found that the number of bees in the field increases at the beginning of the day and diminishes as the day closes. Between these two periods of the day there is a period during which the total number of bees in the field at any particular time is reasonably near a constant number. For this period of the day it may be assumed,[3] for the purpose of estimating the duration of flight, that the two lines are parallel and that the above formula is applicable. To reduce the experimental error arising from this assumption, a period of flight is selected when the number of bees in the field at each reading in this period is known to be very near a constant number. The average of the number of bees in the field at each of the readings in this period is taken as the constant number (f) in the above formula. The number n may be taken from either the outgoing or the incoming totals, thus giving two answers for the duration of flight which may be used as a check on each other.

This method shows that on any day when the number of bees in the field is large it naturally follows that the flight is long; or, conversely, whenever the duration of each trip is short the number of bees in the field is relatively small. (Compare Tables 3 and 4.)

Care must be exercised in the selection of the data to be used in the determination of the average duration of each voyage, for if there has been a large loss in the number of bees which went to the field, the figures would at first glance suggest that the number of bees in the field, instead of remaining constant, is continually increasing, thus giving a larger figure for the average duration of each trip.

The data used for the determination of the average duration of each trip have been arranged (Table 2) to show the figures used in the calculations for each of the days given.

The probable error of the average was determined according to Bessel's formula, $0.6745\sqrt{\frac{\Sigma d^2}{n(n-1)}}$, and shows the precision of the assumed constant number of bees in the field for each of the days given. To facilitate comparisons the probable error of the average has also been expressed as a percentage of the average.

Since there is a direct ratio between the average duration of the voyages and the average number of bees in the field during the period under consideration, it naturally follows that the probable percentage error of the average duration of the voyages, given in the last two columns of Table 2, is liable to the same probable percentage error as the average number of bees in the field. The remainder of the table is self-explanatory.

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[3] The straight line method has been applied to the data for May 15, July 9, and July 10, following the general formula—

$$\text{(I)}\quad \Sigma n + \Sigma x(m) = \Sigma y$$

$$\text{(II)}\quad \Sigma x(n) + \Sigma x^2(m) = \Sigma xy,$$

solving for m and n and substituting in $y = n + mx$, to determine the two points which fix the straight line sought.

For May 15, the straight line representing exits begins at number 4,501 and ends at 36,883, and gives 15.27 minutes as the average duration of the trips; the straight line representing returns begins at 3,133 and ends at 35,111, and gives 15.46 minutes as the average duration of the trips. For July 9 the exit numbers are 6,486 and 17,908, and the resulting average duration of trips 93.78 minutes; the numbers for the returns are 2,742 and 14,510, and the average duration of trips 91.20 minutes. For July 10 the exit numbers are 5,114 and 14,339, and the average duration of trips 102.13 minutes; the numbers for the returns 1,965 and 10,876, and the average duration of trips 105.74 minutes.

This method shows that the lines for the three days diverge somewhat as the time progresses. The average duration of the trips calculated on these lines differs so slightly from the figures obtained by the former method (see Table 2) that for the purposes of this paper, where no close comparisons in the average duration of the voyages is attempted, the formula $x = \frac{tf}{n}$ derived above has been applied directly to the original data in the compilation of Table 2.

It will be noted that the average duration of the voyages was determined with a probable error ranging from less than one-half of 1 per cent to about 7 per cent, the average probable error being 2.45 per cent.

The number of days in the honey flow on which the average duration of the voyages could be determined with full confidence in the figures was small, owing not only to the fact that the honey flow in 1922 was short but also to the fact that it occurred very early in the season, when relatively more difficulties in connection with the apparatus had yet to be overcome. With changing weather conditions the duration of the voyages can be determined more conveniently by the graphic method, which, although not so accurate, is correct to about 3 minutes for the scale used in studying the data.

A survey of a few days (Table 2) shows that the average duration of the voyages varies considerably. The shortest average flight over a considerable period of time is that which occurred on April 20, 8.92 minutes, and the longest that of July 10, 103.92 minutes. Every gradation between these limits occurred. It will be noted that during the dearth of July the average duration of each flight is much longer than during the honey flow; and yet there are days in July when the duration corresponds very closely with such honey flow days as May 8 and 9.

It will be noted also that the duration of the voyages on May 8 and 9 was from two to three times as long as it was on May 15 and 17, and yet all four days (Table 1) were days of fairly good to good honey flow. This great difference can be attributed only to the nature and distribution of the honey plants. On May 8 and 9 the bees are working on the black locust (*Robinia pseudacacia*) entirely. The tuliptree (*Liriodendron tulipifera*) was not yet secreting nectar. On the 15th and 17th only the tuliptree was secreting, the black-locust blooms having been destroyed by a heavy rain on the 14th. The distribution of the trees of these two species in the immediate vicinity of the hive shows roughly that the black-locust trees most accessible are on the average about three times as far away as the nearest available tuliptrees. The structure of the flower of the black locust undoubtedly also contributes to lengthening the average duration of the voyages by requiring a greater exertion from the bee in securing its load of nectar.

The data for May 15, June 6, and July 25 (Table 2) show that the duration of the flights may sometimes vary considerably within the same day. Under uniform conditions, however, it is usually very constant for the greater part of the day's flight.

Graphs (figs. 11, 12, and 13) have been drawn to show in greater detail these variations in the duration of the trips for May 15, a day of good honey flow from tuliptree; for July 10, a day in the dearth; and for May 9, a honey-flow day with locust secretion, with flights of intermediate length. Owing to the heavy flight which occurred on May 15, it has been necessary to cut the graph into three sections in order to draw it to the same scale as the graph for July 10. These sections should be joined so as to give a continually ascending curve such as is shown in Figure 12 for July 10. These curves show that at the commencement of flight the duration of the trips is relatively short, soon to be followed by the balanced condition previously described, when the outgoing bees equal the returning bees in number. Again, as flight closes, a considerable shortening of the duration of the trips is shown. On May 15 (fig. 11), at 3.30 p. m., the two curves, representing the accumulated totals of bees emerging and bees returning, come together, to diverge immediately to a resumption of the previous condition of parallelism. This convergence with an immediate divergence was occasioned by a threatening storm, illustrated in a previous curve (fig. 4), which sent all the bees in the field back to the hive and necessitated an abrupt shortening of the duration of the voyage. At the end of the day the incoming curve, instead of ending below the outgoing curve, crosses it, the vertical distance between the ends of the two curves representing the accumulated experimental error for this day, when 467 more returns than exits were registered. This error has naturally tended to reduce the distance between the two curves, making the apparent duration of the voyages shorter than the real duration. To obtain some idea of the magnitude of the error produced in the determination of the duration of the trips in the period

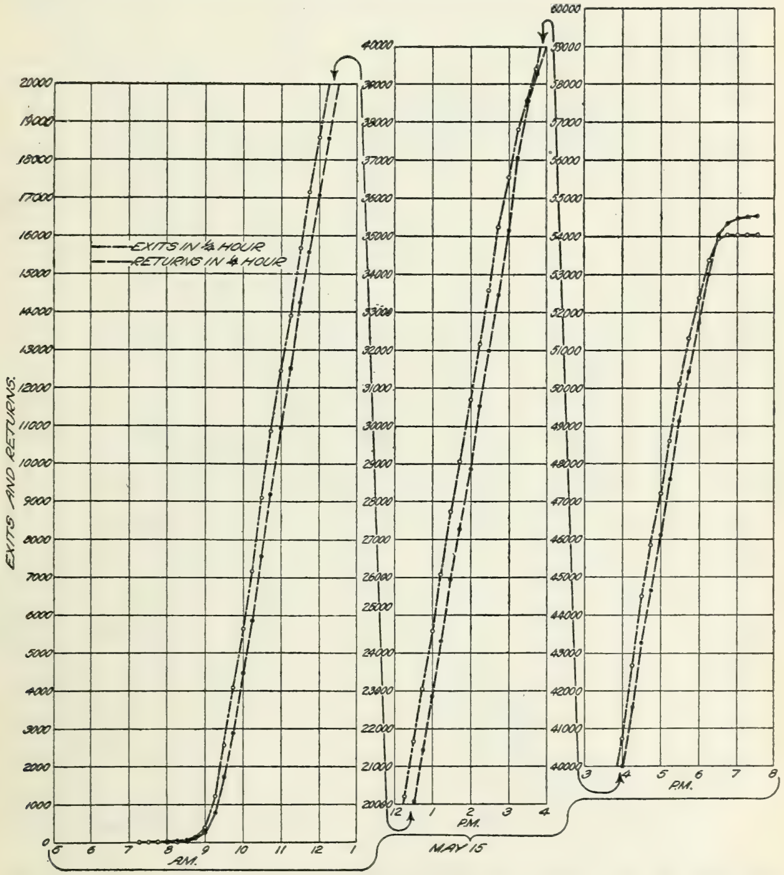

FIG. 11.—Graph representing flight data for May 15, 1922, a day of good flow of tuliptree honey

from 4.15 to 5.15 p. m., the generous assumption may be made that all this error accumulated between 4 p. m. and 7.30 p. m. Applying a correction under this assumption to the number of bees in the field and the returns for this period, it is found on calculation that the duration of the voyage has been increased by 0.39 minute, still showing that the average duration of the flight has been reduced after the occurrence of the threatening storm. This error, however, should properly have been distributed over the whole day, so that its magnitude was actually much below the above figure.

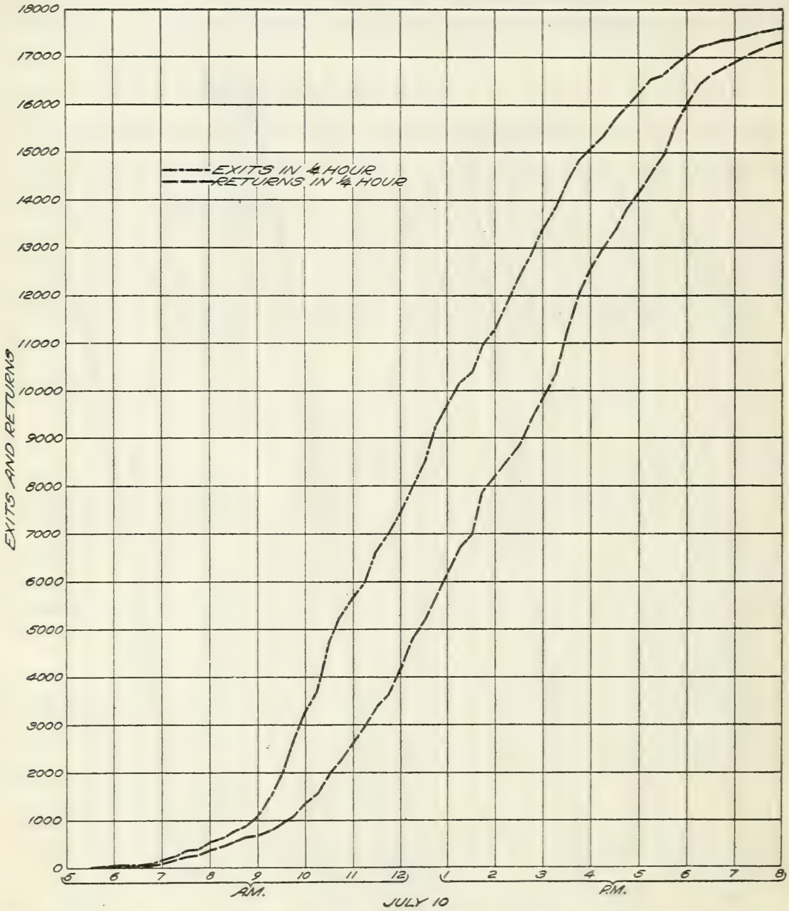

FIG. 12.—Graph representing flight data for July 10, 1922, a day of honey dearth

In attempting to determine what factors are involved in this reduction in the duration of the trips, three things are suggested: (1) That the lower temperature prevailing after the storm stimulated the bees directly; (2) that the lower temperature and the conditions during and after the storm stimulated a relatively heavier secretion, enabling the bees to load more rapidly; or, perhaps, (3) that since fewer bees were visiting the flowers during the threatening storm, relatively more nectar was available to them on the resumption of optimum conditions for flight. The third factor seems the most probable.

July 10 is a good example of a day of great dearth with long flights (fig. 12). The average duration of the voyages in the period from 10.45 a. m. to 3.30 p. m. on this day was 1 hour and 43 minutes. During a portion of this period (from 12.36 to 1.15 p. m.) all the bees (about 1,400) which set out from the hive were absent for as long an interval as 1 hour and 54 minutes. The curve shows a gradual lengthening of the duration of the trips from 15 to 36 minutes between 7 and 8.45 a. m., followed by rather sudden lengthening of the trips from 36 minutes to 106 minutes between 8.45 and 10.45 a. m., which is the beginning of the period of approximate flight equilibrium mentioned above. At the end of the day, as the flight activity comes to a close, a gradual shortening of the duration of the trips is noted. A comparison of the evening shortening with the morning lengthening in the duration of the voyages shows that the lengthening in the morning is somewhat sudden, whereas the shortening in the evening is more gradual. These characteristics were noted on all the days studied. The

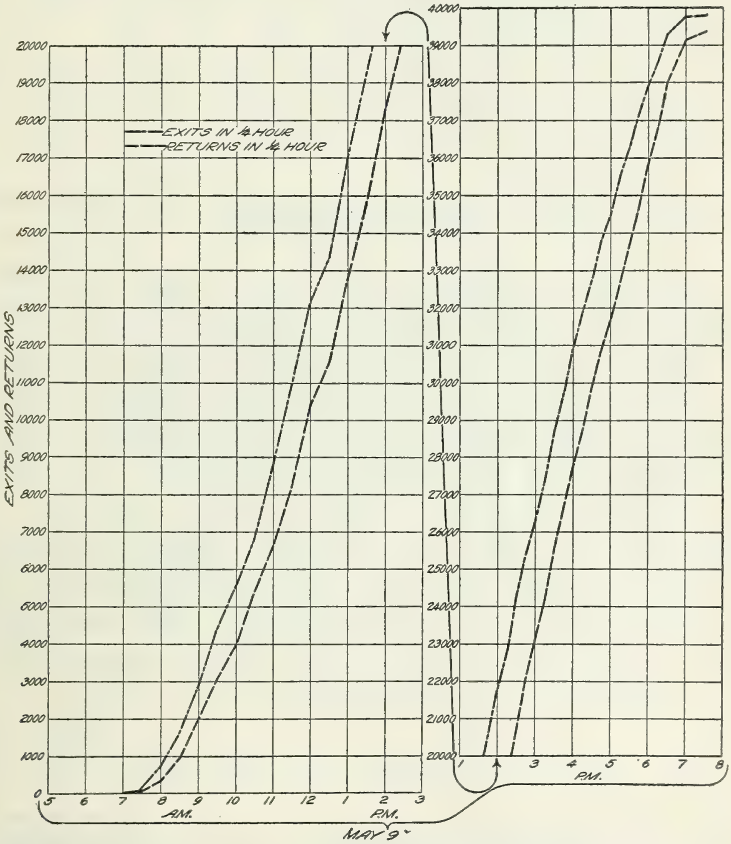

FIG. 13.—Graph representing flight data for May 9, 1922, a day of good flow of locust honey

necessity of a shortening of the voyages as dusk approaches is apparent, but the cause of the short voyages at the beginning of the day's flight is problematical. It may be that these short trips in the dearth are those made by the water carriers.

The flights which occurred on May 9 (fig. 13) when locust honey was available, were intermediate between those given above, their average duration in the period of equilibrium being 42 minutes. The bees were obliged to travel a considerable distance. The details of the variation for this day are easily interpreted from the figure, and need not be explained in full. The method of interpretation is the same as for the examples given above.

These data also indicate that when conditions for a maximum secretion of nectar occur, enabling the bees to gather their loads rapidly and return quickly to the hive, there are relatively more bees within the hive. The significance of this fact with reference to swarming is apparent.

A LIMIT TO THE NUMBER OF TRIPS AND THE TIME SPENT WITHIN THE HIVE

To determine the number of trips which the bees of a colony of honeybees make in the course of any particular day, it is necessary to know the total number of exits (or returns) for the day and the total number of bees which are participating in the flight on this day. Owing to the limited time available for this investigation, no attempt was made to manipulate the colony periodically so as to take a census of the field bees. With the figures available, however, a lower limit to the number of bees participating in the flight is given by the average number of bees in the field, giving in turn an upper limit to the number of trips each bee could make. For example, May 15 (9.45 to 3) the average number in the field is 1,567, so that during this period each bee could not make as many as 32,492÷1,567=20.74 trips, for to maintain this rate these 1,567 bees would have to go in and then out of the hive immediately.

TABLE 4.—*Record of exits and returns, total and per quarter hour, and of bees in the field, July 10, 1922*

Time	Total exits	Total returns	Bees in field	Exits in one-fourth hour	Returns in one-fourth hour
			Number	*Number*	*Number*
5. 30	0	0	0	0	0
5. 45	4	2	2	4	2
6. 00	18	11	7	14	9
6. 15	32	19	13	14	8
6. 30	46	31	15	14	12
6. 45	63	41	22	17	10
7. 00	160	73	87	97	32
7. 15	225	147	78	65	74
7. 30	332	219	113	107	72
7. 45	398	269	129	66	50
8. 00	503	360	143	105	91
8. 15	612	438	174	109	78
8. 30	770	525	245	158	87
8. 45	887	609	278	117	84
9. 00	1, 044	675	369	157	66
9. 15	1, 461	785	676	417	110
9. 30	1, 923	907	1, 016	462	122
9. 45	2, 604	1, 050	1, 554	681	143
10. 00	3, 240	1, 310	1, 930	636	260
10. 15	3, 674	1, 513	2, 161	434	203
10. 30	4, 699	1, 946	2, 753	1, 025	433
10. 45	5, 212	2, 201	3, 011	513	255
11. 00	5, 610	2, 595	3, 015	398	394
11. 15	5, 965	2, 981	2, 984	355	386
11. 30	6, 600	3, 349	3, 251	635	368
11. 45	6, 971	3, 613	3, 358	371	264
12. 00	7, 381	4, 133	3, 248	410	520
12. 15	7, 930	4, 792	3, 138	549	659
12. 30	8, 469	5, 117	3, 352	539	325
12. 45	9, 242	5, 646	3, 596	773	529
1. 00	9, 662	6, 134	3, 528	420	488
1. 15	10. 197	6, 692	3, 505	535	558
1. 30	10, 382	6, 955	3, 427	185	263
1. 45	10, 965	7, 848	3, 117	583	893
2. 00	11, 290	8, 197	3, 093	325	349
2. 15	11, 851	8, 509	3, 342	561	312
2. 30	12, 405	8, 849	3, 556	554	340
2. 45	12, 828	9, 366	3, 462	423	517

TABLE 4.—*Record of exits and returns, total and per quarter hour, etc.*—Con.

Time	Total exits	Total returns	Bees in field	Exits in one-fourth hour	Returns in one-fourth hour
			Number	*Number*	*Number*
3. 00	13, 357	9, 816	3, 541	529	450
3. 15	13, 831	10, 354	3, 477	474	538
3. 30	14, 378	11, 265	3, 113	547	911
3. 45	14, 820	12, 051	2, 769	442	786
4. 00	15. 082	12, 570	2, 512	262	519
4. 15	15, 334	13, 007	2, 327	252	437
4. 30	15, 688	13, 370	2, 318	354	363
4. 45	15, 986	13, 812	2, 174	298	442
5. 00	16. 212	14, 149	2, 063	226	337
5. 15	16, 508	14, 574	1, 934	296	425
5. 30	16, 609	14, 944	1, 665	101	370
5. 45	16, 861	15, 538	1, 323	252	594
6. 00	17, 040	16, 022	1, 018	179	484
6. 15	17, 225	16, 451	774	185	429
6. 30	17, 298	16, 654	644	73	203
6. 45	17, 350	16, 788	562	52	134
7. 00	17, 394	16, 907	487	44	119
7. 15	17, 463	17, 056	407	69	149
7. 30	17, 533	17, 191	342	70	135
7. 45	17, 584	17, 266	318	51	75
8. 00	17, 619	17, 305	314	35	39

On any day when the conditions governing flight are fairly uniform throughout the course of the day, it has been found, as has been previously explained (p. 26), that sooner or later the flights approach a state of equilibrium (Tables 3 and 4), the group of bees in the field remaining almost constant, the flow of bees to this group being balanced by the flow from it. The magnitude of the group of bees participating in flight, but remaining in the hive, and which will eventually reissue therefrom, must therefore also remain approximately constant. Then, again, just as there is a direct ratio between the number of bees in the field and the time they are spending in the field, so must there also be a direct ratio between the number of bees in the hive taking part in the flight and the time they spend in the hive between the trips during the period of equilibrium.

If we assume that on May 15 there were as many bees in the hive participating in the flight as there were bees in the field, the bees were spending as much time in the hive as out of it. The inferior limit to the number of bees participating in the flight on this day would then be 3,134 bees, and the maximum limit to the number of trips would be 10.27. This figure 3,134 seems to be a relatively small fraction of the total colony, which at this time must have consisted of some 5 pounds of bees (about 25,000). These figures seem to suggest, therefore, that even in a strong honey flow the bees spend more time in the hive between the voyages than they do on the voyage itself.

THE DEATH RATE OF THE COLONY

Since the mechanism of the gates prevented the bees from carrying out their dead, these collected behind the incoming gates, where they were counted and removed every time the gates were detached for cleaning. This meant that at certain periods they were counted every day and at others once in four or five days, depending upon the condition of the instruments. On only one occasion did the count ever exceed 100 bees. The total number of bees which died in the hive while the instruments were attached was 1,060. This is 1.63 per cent of the total number of bees (65,178) recorded lost from all causes. In handling the apparatus the writer has gained the rather indefinite impression that as a rule there is a greater error on the outgoing gates than on the incoming. If this is true, the actual percentage of deaths in the hive is slightly above this figure.

The records for 89 days, which have been chosen as representative of the data obtained, show that of the bees which left the hive (2,434,666), 3.16 per cent did not return. If the assumption is made that the errors in the counts of exits and entrances balance each other, this would mean, since every exit represents a trip by a bee, that one bee dies after every 31.65 exits have occurred, or that each bee makes 31.65 trips before death overtakes it in the field.

It is generally accepted that the mortality of honeybees is in proportion to the amount of work which they do. It is also evident that during the night, when flights do not occur, all deaths will take place within the hive, and during the active season there is usually a period of 10 hours daily when there are no flights. If, therefore, about 98 per cent of the deaths from the colony occur in the field, this indicates that most of the deaths occur during the approximately 14 hours of flight. These data suggest that the energy expended by the bees in flight and in activities outside the hive greatly exceeds that expended within the hive. This conclusion is to be anticipated from the enormous amount of energy which must be expended in flight. Assuming (1) that a field bee is away from the hive one-half of the flying hours, (2) that a death rate of 2 per cent occurs within the hive, and (3) that there is a 14-hour period of flight for the day, the chance of a bee dying outside the hive during any given hour of the period of flight is about 120 times as great as the chance that death shall occur within the hive. This at least suggests that for any given instant the expenditure of energy on flight or away from the hive is about 120 times as great as that expended by a single bee within the hive.

THE BEHAVIOR OF THE BEES TO THE INSTRUMENTS

In the initial stages of the experiment, although about 2,000 bees passed satisfactorily through the experimental model, the reaction of the colony as a whole to the complete set of instruments was entirely problematical. The success or failure of the experiment, therefore, depended upon this reaction. The plan of placing the outgoing gates above the incoming ones, so that the actual entrance apertures were only about 2 inches below the exit apertures, proved very satisfactory, only an occasional bee attempting to enter the hive by an outgoing gate.

Considering the tunnel of the contact device as a hole in the wall of the hive which drops a distance equal to twice the height of a bee while the latter passes through it, the delay produced by these instruments is negligible and the only abnormality introduced is the jar of the tunnel meeting the lower stop. Owing to the fact that any hesitancy of a bee in walking out of the tunnel prevents another from using this aperture, a net delay on all the apertures ensues. The return movement of the tunnel to receive the next bee is a minor source of delay when compared with that produced by the hesitancy shown by some of the bees in selecting the aperture by which they finally enter. Probably this hesitancy on the outgoing gates is not so marked. It has been impossible to determine the actual delay produced. On seeing the rapidity shown on certain occasions by some of the bees when leaving the outgoing gates, one would not hesitate to state that these bees left the hive as rapidly as they do normally. The hesitancy mentioned above was greater when there were fewer bees on the alighting board, as, for example, before or after the main flight of the day or on dull, overcast days. On leaving the tunnel some of the bees would stop to fan their wings, and many others might simply clean their antennae or perform some minor movement and then fly away, as if everything were normal.

At the beginning of the experiment the binding posts on the instruments were exposed. Bees in walking over these could short-circuit the current, getting an electric shock to which they reacted in an interesting manner. They did not cause a record to be made by the cyclometers when this occurred. The excitement of the first bee to get a shock soon drew others to the scene of the phenomenon. Some would approach the binding posts with apparent caution and on getting a shock would retreat and then return to repeat the operation again and again, until finally a few superinfuriated ones went to war against this invisible enemy by attempting to deposit their darts in the brass work. The stings usually found a final lodging place in the rubber insulation on the wires. These efforts being of no avail, other bees proceeded to propolize the instruments, thus perhaps utilizing for the first time the insulating value of propolis. This abnormal behavior was discontinued when the binding posts were covered with cotton wool.

The light penetrating the outgoing gates through the glass windows attracted the bees so strongly that two bees sometimes attempted to enter the tunnel at one time, thus retarding or preventing its drop and their egress from the hive. By darkening the glass, thus reducing the intensity of the light, a satisfactory action was brought about, which increased the former capacity of the instruments by about four times. This behavior was entirely contrary to all expectations, for in the design of the instruments an attempt was made to get the maximum of light to enter the outgoing tunnels. In actual practice, to promote a correct action of the instruments, this light was almost completely shut out by the black paint placed on the glass. It is interesting to note that the bees used the tunnels with no apparent hesitation, although the light intensity was far below normal.

During the hot weather following the main honey flow a large number of bees, instead of returning to the entrance apertures as normally, collected on the platform of the scales under the hive. This occurred especially about midday and in the early afternoon and they would remain in this place all night, apparently held there by the hive odor which emanated from the ventilator in the bottom of the hive about 14 inches directly above them. With the exception of the above incidents, all of which were eventually avoided, at no time, so far as could be determined, did these instruments produce any abnormality in the behavior of the colony.

The highest rate at which the instruments ever worked was in one quarter of an hour preceding a storm, when each ingoing gate admitted in these 15 consecutive minutes an average of 14 bees a minute.

CONCLUSIONS

A satisfactory device for counting bees as they journey to and from the hive would open up a new field of apicultural research. In addition to throwing light on many interesting questions, its most practical application would perhaps be in a study of nectar secretion, as it affords a measure of the variations in flight and in the duration and number of trips which the bees make, as well as their average daily load, facts which are to a large degree a reflection of the nectar conditions in the field.

This study demonstrates the feasibility of obtaining data on problems pertaining to the flight of bees by means of an automatic recording mechanism. As far as can be ascertained, the mechanical principles on which the design was made are in general correct. Much work, however, on further details is desirable.

Owing to factors incidental to any new and untried mechanism, a variable experimental error was introduced which as far as can be determined for any day varied from 0.08 per cent to as much as 27.81 per cent. The magnitude of this error, though prohibitive for certain phases of the study, was not entirely so for others, and by a selection of those days on which it was obviously at a minimum, information may be obtained which is practically as valuable as if no error were incurred.

A survey of the total daily exits and returns for the period of the observations shows that a factor or group of factors can reduce the total number of possible exits by an amount varying from total prohibition of flight to a fraction of 1 per cent. A threatening storm, for instance, of but one hour's duration, reduced the possible flight on one day in the honey flow by 7.41 to 9.67 per cent.

Comparatively few data have been obtained on the effect of wind on the flights. On one day, however, a wind velocity of 16 to 21 miles per hour during the hours 9 a. m. to 6 p. m. reduced the possible maximum flight by 28.53 per cent.

Under a particular set of conditions the temperature at which the day's flight commences is uniformly near a certain definite temperature, but this definite temperature is not always the same. In April it was from 12° to 14° C. and in May from 16° to 18° C. On dull days this temperature was usually 2° higher. The internal conditions of the colony govern this temperature somewhat, a strong colony commencing flight at a lower temperature than does a weak one.

There is a considerable variation in the hour and temperature at which the peak of the flight in the honey flow occurs. No conclusive evidence has been obtained that under similar conditions a good honey flow induces the bees to go out in large numbers at a lower temperature than they would if no nectar were available. The temperature at which the flights in the evening begin to slacken was without exception higher by from 1° to 9° C. than the temperature at which flight began in the morning. Days which appear to be similar in every respect but which show a variation of as much as from 10 to 25 per cent in their total flights are found to differ on account of a lower temperature in the early part of the day.

Under honey-flow conditions the total exits proved to be three to four times as great as they were at any other time of the investigation.

A typical flight, where all conditions are fairly uniform and favorable throughout the day, is a gradual to rapid increase in the successive numbers of bees which set out from the hive, to be followed by a condition of equilibrium in which the outgoing numbers are balanced by almost equal incoming numbers. Under these conditions it was found that the number of bees in the field remained nearly constant.

Under honey-flow conditions the main flight to the field usually occurred some three to four hours earlier than in the dearth.

From the graphs representing the progressive totals of outgoing and incoming bees the average duration of each flight at any period of the day can readily be determined. During the main flight for the day, when usually a balanced condition of flight is maintained, these graphs are represented by two almost parallel straight lines. The morning and evening flights are very much shorter than those that take place in the main period of the day's flight, a variation of as much as from 15 minutes to 1 hour and 43 minutes occurring in one day. Taking all the days for which the average duration of the trips was determined, it is found that this duration varies from 8 minutes to as much as 1 hour and 54 minutes. In the honey flow the trips are much shorter than they are in a dearth.

Although the colony was not manipulated periodically so as to take a census of the field bees, the figures available seem to show that even in a heavy honey flow the bees spend more time in the hive between trips than they do on the trip itself.

By knowing the amount of nectar gathered on any day and the total number of bees which return, the minimum weight of the average load carried by each bee can be estimated. The highest minimum average load obtained was on May 22, when 44,597 bees averaged 25.3 milligrams each. Although there is a close relation between the amount of nectar gathered on any day and the amount of nectar available to the bees, this relation is not absolute. The average load per bee is the true indicant of the available nectar.

Assuming that the errors on the outgoing and incoming gates balanced each other, the records for 89 days show that of the 2,434,666 bees which left the hive 3.16 per cent did not return. This would mean that on an average a bee makes about 31.65 trips before death overtakes it.

Of the 65,178 bees lost from all causes 1.63 per cent died in the hive.

Except for certain difficulties which were eventually overcome, at no time during the three and one-half months of this investigation did these instruments produce any discernible abnormality in the general behavior of the colony. The highest rate at which the gates were ever worked was during a quarter of an hour preceding a storm, when each incoming gate admitted in these 15 consecutive minutes an average of 14 bees per minute.

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